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COMPETITION FOR FOOD BY BIRDS OF PREY

BY DAVID LACK, *Edward Grey Institute of Field Ornithology, Oxford*

1. INTRODUCTION

Lotka and Volterra provided equations for the interaction of two species competing for the same food supply, and from these Gause (1934) developed the thesis that two species with the same ecology cannot persist together in the same region. (For detailed references to the mathematical aspects of interspecific competition, see Crombie (1945).) Although both the mathematical treatment and Gause's laboratory experiments refer to monophagous species, the examples cited by Gause to illustrate his principle in nature were drawn from polyphagous animals. Further, I have shown that ecological isolation holds among polyphagous passerine and various other bird species in Europe and on oceanic islands (Lack, 1944, 1945*a*, 1946). Detailed food studies by Uttendörfer (1939), chiefly in Germany, provide the raw material for a parallel analysis of the extent to which ecological isolation may occur in the European birds of prey, the Falconiformes (falcons, eagles, buzzards, etc.) and Strigiformes (owls). The birds of prey are of particular interest as regards competition for food because they have no serious predators (omitting man), and in a natural state they are presumably limited in population density by their food supply. The present paper shows that most of the species concerned do not compete for food, thus supporting Gause's thesis, but there is an apparent striking exception, for which an explanation is suggested.

2. DIVERSITY OF PREY

On reading Uttendörfer's lists, the first impression is of the diversity of foods taken by each predator. Thus 43,211 individual animals eaten by the sparrow-hawk (*Accipiter nisus*) consisted of 12 species of mammals and 132 species of birds, while 7335 preys of the goshawk (*A. gentilis*) consisted of 15 species of mammals and 125 of birds. Most other Falconiformes take a similar wide variety of species, and the same is true of most Strigiformes. For instance the tawny owl (*Strix aluco*), three-quarters of whose diet consists of small mammals, has also been recorded taking 92 species of birds, 4 species of reptiles, 11 species of Amphibia, 10 species of fish, and a great variety of insects. Even the specialized honey buzzard (*Pernis apivorus*), which subsists primarily on the contents of wasps' nests, also takes a variety of small mammals, birds, reptiles, Amphibia and many orders of insects.

From the standpoint of interspecific competition and Gause's thesis, only the common food items are important. These have been summarized in the Appendix for all the predatory species which breed regularly in Germany, and they show that each of these species depends primarily on only a few kinds of prey.

3. CLOSELY RELATED SPECIES

As pointed out by Darwin, competition is likely to be most severe between closely related species, hence such forms are of special interest and will be considered first. For convenience, species are here regarded as closely related when a modern taxonomist such as Witherby (1938–9) places them in the same genus. The summary in the Appendix shows that no two congeneric species of German predatory birds compete for the same food supply. Either they differ in habitat, in which case their hunting methods and the size of their prey are sometimes similar, or they live in the same habitat, in which case their hunting methods and/or the size of their prey are different. This confirms the general conclusion of earlier papers (Lack, *loc. cit.*).

In the earlier papers, particular attention was given to species-pairs which live in the same habitat and have similar feeding methods, but differ conspicuously in size. The goshawk (*Accipiter gentilis*) and sparrow-hawk (*A. nisus*) provide a good example, as their habitat and hunting methods are very similar, but the former species is much larger than the latter (wing measurements of females 340–375 and 230–240 mm. respectively). The data in the Appendix show that the goshawk mainly takes birds of larger size than does the sparrow-hawk, and that these two predators do not have a single important prey-species in common—a prey-species being reckoned as important when it provides at least 5% of the diet. Incidentally, a warning may be given against comparing prey-lists which lack an indication of frequencies (as in Witherby *et al.* 1938–9). Of the 140 species of prey listed by Uttendörfer for the goshawk, as many as 61% are also taken by the sparrow-hawk, but this superficial impression of overlap is highly misleading.

A similar size-differentiated species-pair occurs in the genus *Falco*, with the large peregrine (*F. peregrinus*) (♀ wing 344–370 mm.) and smaller hobby (*F. subbuteo*) (♀ wing 265–280 mm.). The peregrine

mainly preys on birds of larger size than does the hobby, though they show a small overlap in that both take the skylark (*Alauda arvensis*); the hobby, unlike the peregrine, also takes many insects. A third member of the genus, the kestrel (*Falco tinnunculus*), overlaps extensively in habitat with the other two, but it differs markedly from them in its hunting methods and food, as it searches from a high perch or by hovering in the air, and picks its prey, chiefly voles, off the ground, whereas the other two species mainly take flying prey on the wing.

The two species of *Aquila* have almost completely different diets, the lesser-spotted eagle (*A. pomarina*) feeding mainly on frogs, also on reptiles, and the golden eagle (*A. chrysaëtus*) mainly on hares (*Lepus* spp.) and grouse and ptarmigan (*Lagopus* spp.). The two species of *Milvus* feed on carrion and have certain foods in common, but the black kite (*M. migrans*) takes chiefly fish, which the red kite (*M. milvus*) does not do. The two species of *Asio* have similar hunting methods and take prey of a similar nature, but they do not compete since they mainly frequent different habitats, the long-eared owl (*A. otus*) in wooded country and the short-eared owl (*A. flammeus*) on moors and marshes. Finally there are three species of *Circus*, but for these a definite statement cannot be made, as Uttendörfer's data are inadequate. The hunting methods of the three species are similar, but in the main they frequent different habitats. Also, though marsh and Montagu's harriers (*C. aeruginosus* and *pygargus*) sometimes breed near each other, they differ in size (♀ wing 390–420 and 350–380 mm. respectively), and this is apparently reflected in the size of their prey.

To sum up: omitting one genus because of inadequate knowledge, no two congeneric species of German predatory birds compete for the same food supply.

4. COMPARISON OF SPECIES IN DIFFERENT GENERA

The comparison may now be extended to species in different genera, excluding for the moment the mammal predators, which are treated later. In all, twelve species of Falconiformes are concerned, two in each of the genera *Accipiter*, *Falco*, *Milvus* and *Aquila*, and one in each of the genera *Pernis*, *Pandion*, *Circaetus* and *Haliaeëtus*. The food summaries in the Appendix show that each of these twelve species feeds primarily on different species of prey. The main foods of the eight species in the four former genera were mentioned above, while of the four in the four latter genera, the honey buzzard (*Pernis apivorus*) feeds chiefly on the contents of wasps' nests, the osprey (*Pandion haliaetus*) on fish, the snake eagle (*Circaetus gallicus*) on snakes, and the white-tailed eagle (*Haliaeëtus albicilla*) on large waterbirds.

There are only two apparent cases of overlap in food, and neither of these invalidates the main argument. First, the diet of the kites (*Milvus* spp.) includes many species eaten by other predators, but kites are primarily carrion-feeders, so do not really have similar ecology to the others. Secondly, the tame pigeon (*Columba livia*) is the chief item in the diets of both goshawk (*Accipiter gentilis*) and peregrine (*Falco peregrinus*). But the tame pigeon is an artificial food whose numbers are maintained by man, and without whom it would probably become extinct. If it were eliminated, goshawk and peregrine would not seriously compete for food, though they show a small and unimportant overlap in that both take the starling (*Sturnus vulgaris*). There is a similar small but unimportant overlap in the diets of sparrow-hawk (*Accipiter nisus*) and hobby (*Falco subbuteo*), in that both take skylark (*Alauda arvensis*) and swallow (*Hirundo rustica*). With these insignificant exceptions, the twelve predatory species discussed in this section show no important overlap with each other in diet.

5. PREDATORS ON MAMMALS

So far, Gause's thesis is confirmed. However, the remaining birds of prey present a strikingly different picture, for in five species of Falconiformes and at least five species of Strigiformes, the bulk of the food consists of a single species of prey, the vole *Microtus arvalis*. The percentage of *Microtus* recorded in the diet is given for each species in the Appendix, but the figures are not very reliable, as they vary markedly in different years according to the density of *Microtus*. For instance, Tinbergen (1933) found that in Holland during a good vole year, 80% of the prey of the long-eared owl (*Asio otus*) consisted of *Microtus*, but during a poor vole year the proportion of *Microtus* dropped to 30%. But even though the actual percentage cannot be stated accurately, the fact is clear that *Microtus* forms the primary food of at least ten species of predatory birds.

Not all these ten species compete with each other. As already mentioned, the congeneric species differ in habitat, among *Microtus*-eaters this applying to the two species of eared owl (*Asio*) and (with less supporting evidence) to the three species of harrier (*Circus*). Also, there are a few cases in which the extent to which *Microtus* bulks in the prey may be unnatural and due to man. Man has replaced forests and swamps by grassland and cornfields, the latter being the favourite habitats of *Microtus*. As most of the remaining woods and marshes are small, a woodland bird like the tawny owl (*Strix aluco*) and a marsh bird like the marsh harrier (*Circus aeru-*

ginosus) are brought much closer to the haunts of *Microtus* than they would be under natural conditions. Possibly, too, the proportion of *Microtus* in Uttendörfer's lists is misleadingly high for a few of the rarer species of birds, should the analyses happen to have been made during a vole plague.

Making full allowance for these exceptions, or possible exceptions, there remain about five common species of predatory birds which live in the same habitat and feed primarily on *Microtus*. These are a species of *Falco* (the kestrel), a species of *Buteo* (the buzzard), a species of *Asio* (short-eared or long-eared owl, according to habitat), a species of *Circus* (hen or Montagu's harrier, according to habitat), and often a species of *Tyto* (the barn owl). To complete the picture, one or more species of predatory mammals take *Microtus* as a main food, and several other species of mammals and birds, including the white stork (*Ciconia alba*) (Schüz, 1942), feed largely on *Microtus* when it is very abundant. The habitat in which this takes place, grassland or cornfields, depends for its existence on human activities, but it cannot be argued from this that the situation involved is unnatural. A parallel situation is found on Scottish moorland, where several species of birds and mammals feed primarily on *Microtus agrestis*. Similarly, on tundra, which is unquestionably a natural habitat, there are in any one region up to five species of birds and two of mammals feeding predominantly on the lemming (*Lemmus*). (A list for one region is given later.)

The predators on *Microtus* and lemmings show one, and sometimes two, uncommon adaptations to the huge fluctuations which characterize their prey. First, in most species of birds, annual differences in number of broods and in clutch size are small. But, when their prey is excessively common, the rodent predators commonly raise two broods in the year instead of one, and have clutches of up to double the usual size, while when their prey is excessively scarce, they do not attempt to breed (references in Elton, 1942 and Lack, *in press*). Secondly, emigration (as distinct from migration) is rare in birds, but among predators upon rodents it occurs in short-eared owl (*Asio flammeus*) and snowy owl (*Nyctea scandiaca*). The habit is apparently correlated with periodic food shortage, and as a food shortage is often local, the species may by wandering reach another favourable area, as shown by Reinikainen (1937) in the case of the crossbill (*Loxia curvirostra*). The lemming cycle is not synchronous in all parts of the Canadian Arctic (Chitty, 1945), hence the emigration of the snowy owl may sometimes bring it from a region of lemming scarcity to one of abundance. The presence of such adaptations in these predators indicates that their dependence on rodents has existed for a long time.

Gause's thesis, that when two species compete for the same food supply one must eliminate the other, seems logically unassailable. Even so, one would have tended to reject it if the European species of hawks and owls had shown a marked overlap in their prey in many directions. In fact, however, most such species eat different types of food, and the overlap is confined to a single prey-species, though here the overlap is huge. This suggests that Gause is essentially right, and it is worth inquiring whether the facts for the predators upon rodents cannot be reconciled with theory. In the present state of knowledge, such an inquiry is necessarily tentative, but it seems worth prosecuting, particularly as it suggests lines for future field work.

It was stated in earlier papers (Lack, 1944, 1945*a*) that two species can persist together in the same habitat and eating the same type of food, provided their numbers are kept below the food limit by either predators or disease. Under these conditions, though the two species eat the same type of food, they do not compete for it. (Nicholson (1933) argues further that the two species must have different predators or parasites.) The predators upon rodents do not appear to constitute a case of this type. They have no serious enemies, and though their diseases have not been studied, there is at present no reason for thinking them important. Another possibility may be suggested.

6. TEMPORARY SUPERABUNDANT FOODS

In the Galapagos at the beginning of the rainy season, nearly all the species of Darwin's finches (Geospizinae) eat young leaves and buds, also nectar in tree-flowers. Some weeks later, when the young leaves, buds and flowers have passed, nearly all the finches take sphingid caterpillars, which may be very abundant. A little later the fruits ripen, and most species turn to them. Then the grasses produce seed, and several species find food there. So impressed was I with these successive fashions in food as different foods became abundant, that originally I failed to appreciate that all the finch species have diets sufficiently different to avoid effective competition with each other, and that their beaks are adapted to the feeding differences (compare the accounts in Lack, 1945*b*, 1946).

That many species of birds turn to eat a seasonally abundant food is too well known to require further documentation. Under such conditions, several species are often seen feeding together. In most cases, the abundance lasts for only a brief period, e.g. the time of fruiting, or the caterpillar stage of a moth, though it is often repeated annually. To cite just one further case, from the sea instead of the land, krill (euphausiid Crustacea) form the staple summer

food of several species of both marine mammals and marine birds in the Antarctic. I believe that the case of *Microtus* and *Lemmus* is fundamentally the same as these others, but with the important difference that abundance continues for 2–3 years at a stretch instead of for a brief season. I propose that the term 'temporary superabundant foods' be used for such cases. I suggest that the facts are reconcilable with Gause's thesis, because the foods in question are temporarily so much more abundant than the requirements of their consumers that the latter do not effectively compete with each other while eating them; and that this may still be true even if the food in question temporarily provides the bulk or even the whole of the diet of the species involved.

Further observations are needed to prove whether the foods in question are superabundant, but this is certainly the impression when one sees the Galapagos finches eating buds, or Antarctic penguins and whales eating krill, or English woodland birds eating geometrid caterpillars, or Arctic predators eating lemmings. The very use of such a term as 'vole plague' implies superabundance. A further point is probably essential, that the eventual decrease of the superabundant food is not brought about primarily by its consumers. This is obvious in the case of buds which turn into leaves, fruits which fall, or caterpillars which pupate. The cause of the periodic *Microtus* or lemming minimum is not certainly known (Elton, 1942). Climatic cycles, shortage of vegetable food, and particularly disease have been suggested, acting either separately or together. However, all authors seem agreed that predators are not responsible. If they had been, they would presumably be competing at the time of the rodent maximum and subsequent decrease, and the views suggested here would not be tenable.

While, it is argued, the consumer species do not effectively compete with each other when eating the superabundant food, the situation is potentially quite different as soon as the food in question becomes scarce. The small birds which eat buds or caterpillars when in season do not require further discussion here, because such foods are extremely temporary, while it has already been shown in earlier papers that many birds of this type are isolated from each other ecologically (Lack, 1944). The *Microtus* and lemming predators are in a different category, as for 2–3 years they have been preying almost entirely on a single species, which suddenly becomes extremely scarce. If Gause's views hold, one would expect that in any one region each predatory species would now turn to different prey. This possibility requires investigation. Uttendörfer's data are unfortunately not adequate to decide the point. He lists all the known preys of each predator, but many of these prey-lists were made during times of *Microtus* abundance, and it does not follow that the same additional or alternative preys are important when *Microtus* is scarce. The possible existence of differences in diet is suggested by the fact that, in any one habitat and district, all the *Microtus* predators belong to different genera and have rather different hunting methods; none are closely related species with similar hunting methods. However, more cannot be said on this subject at present.

Rather more is known about the alternative prey of the lemming predators in eastern Greenland (Manniche, 1910; Pedersen, 1930, 1934). Here six carnivorous species, all in different genera, depend for food primarily on the lemming when the latter is common, viz. arctic fox (*Alopex lagopus*), ermine (*Putorius ermineus*), raven (*Corvus corax*), snowy owl (*Nyctea scandiaca*), gyr-falcon (*Falco rusticolus*), and long-tailed skua (*Stercorarius longicaudus*), while a seventh species, the glaucous gull (*Larus hyperboreus*), also takes many lemmings when they are common. During a lemming minimum, and in coastal districts at all times, the arctic fox is a general predator and carrion feeder, particularly taking adults and eggs of the little auk (*Alle alle*), which it stores for the winter, and also following after bears for their leavings. The ermine has not been recorded taking any other important prey during a lemming minimum, when Pedersen (1934) says that it does not breed. It takes young birds, and occasionally carrion. The raven has an extremely varied diet, including much carrion, and occurs in many regions where there are no lemmings, though feeding almost exclusively on the latter when they are abundant. The snowy owl occasionally takes arctic hare (*Lepus timidus*) and ptarmigan (*Lagopus mutus*), but these do not seem important to it; it depends primarily on lemmings, and when these fail it emigrates, which may bring it to a region where lemmings are common, while in years of widespread lemming failure, it emigrates south out of the range of the lemming. The gyr-falcon feeds on many species of sea-birds, and it can exist without lemmings, though taking them when abundant (see also Dementiev & Gortchakovskaya, 1945). The long-tailed skua depends on lemmings for breeding, and when they fail it leaves the breeding grounds prematurely, but except when breeding it is a sea-bird, forcing arctic terns (*Sterna macrura*) to vomit up what they have caught, and also feeding on carrion and other things. The glaucous gull is a coastal species, feeding on crabs, fish, carrion, birds' eggs, etc.

To sum up: while further data are required, it seems possible that the seven lemming predators of eastern Greenland have different alternative prey when the lemming is scarce.

A further important point requiring study is the extent to which the predators upon *Microtus* and

lemmings compete with other predatory species during the period when they are taking alternative prey. Tinbergen (1933) has shown that when *Microtus* is common the long-eared owl (*Asio otus*) takes very few small birds, but when *Microtus* is scarce there is a marked increase in the proportion of small birds in the diet, including many house sparrows (*Passer domesticus*) and other species which are a staple food of the sparrow-hawk (*Accipiter nisus*). During the latter periods one must conclude that the long-eared owl and sparrow-hawk are to some extent in competition, and if such competition persisted for long enough, one would expect the sparrow-hawk to eliminate the long-eared owl. However, it would seem that, before this can happen, voles have increased in numbers and again provide the staple food of the long-eared owl.

This case has much theoretical interest, as it suggests a way in which two or more species might be able to persist together although their numbers are limited by their food supply and although they eat the same foods. Reduced to its simplest terms, one may postulate three predatory species, *A*, *B* and *C*. *A* feeds on food *a*, *B* feeds on the temporarily superabundant food *b* for most of the time, but turns to food *a* when *b* is scarce, while *C* also feeds primarily on food *b* but turns to another food *c* when *b* is scarce. Species *B* does not compete with species *C* because their common food *b* is temporarily superabundant, while it competes temporarily with species *A* for food *a*, but not for long enough at one time to be eliminated by species *A*.

In conclusion, it should be kept in mind that the mathematical analyses of population interactions have been based on monophagous species. The birds of prey, like most other vertebrate animals, are polyphagous, some highly so, others to a smaller extent, some all the time and others only temporarily. Nevertheless, Gause's thesis of ecological isolation appears to hold good; indeed the only apparent exception occurs in the predators upon rodents, which are much more nearly monophagous than the other groups. Animal ecology badly needs a theoretical basis for studying the interactions of polyphagous species, and the object of this paper is to draw attention to a highly complex problem, rather than to state a solution.

7. SUMMARY

1. Among German Falconiformes and Strigiformes, no two congeneric species compete for food in the same habitat. Further, when species in different genera are compared, no two compete for the same food supply, with the apparent exception of the predators upon the vole *Microtus arvalis*.

2. *Microtus arvalis* forms the staple food of several species of hawks and owls, of which up to five (none congeneric) may occur together in the same habitat. It is suggested that these predators do not effectively compete with each other because for most of the time *Microtus* is superabundant, while, when there is a vole minimum, each predator perhaps turns to different prey. The latter suggestion needs investigation.

3. Parallels are cited with other foods which are temporarily superabundant, and the observations are briefly related to theories of population interaction.

8. APPENDIX

Food lists summarized from Uttendörfer (1939)

A. FALCONIFORMES

1. *Accipiter nisus* (sparrow-hawk): hunts small birds in woods, gardens and villages. Main foods: house-sparrow (*Passer domesticus*) 10%; chaffinch (*Fringilla coelebs*) 8%; skylark (*Alauda arvensis*), yellow bunting (*Emberiza citrinella*) and song thrush (*Turdus ericetorum*), each 7%; great tit (*Parus major*), whitethroat (*Sylvia communis*) and swallow (*Hirundo rustica*) each 5%. (43,211 prey examined.)

2. *Accipiter gentilis* (goshawk): hunts in woods, like the sparrow-hawk, but preys on rather larger birds. Main foods: jay (*Garrulus glandarius*) 16%; tame pigeon (*Columba livia*) 16%; partridge (*Perdix perdix*) 11%; wood pigeon (*Columba palumbus*) 8%; starling (*Sturnus vulgaris*) 5%. (7335 prey examined.)

3. *Falco peregrinus* (peregrine falcon): hunts in open, not woods, on prey of same size as does goshawk. Main foods: tame pigeon (*Columba livia*) 27%; starling (*Sturnus vulgaris*) 22%; lapwing (*Vanellus vanellus*) 9%; skylark (*Alauda arvensis*) 5·5%. (In Britain, common on sea cliffs, feeding on sea birds.) (5504 prey examined.)

4. *Falco subbuteo* (hobby): hunts small birds and insects, chiefly in open country with trees. Main bird foods: swallow (*Hirundo rustica*) 29%; skylark (*Alauda arvensis*) 20%; house martin (*Delichon urbica*) 10%—but this takes no account of the large number of insects, mainly Odonata and Orthoptera. (900 vertebrate prey examined.)

5. *Falco tinnunculus* (kestrel): hunts in open country, 89% of the diet being mice, predominantly the vole *Microtus arvalis*. (Over 30,000 prey examined.)

6. *Buteo buteo* (common buzzard): hunts in open country, predominantly on the vole *Microtus arvalis* (66%). (About 15,000 prey examined.)

7. *Milvus milvus* (red kite): feeds in open country, primarily on carrion. Food highly variable, but mainly dead birds of the size taken by goshawk and peregrine (q.v.) and mammals such as hamster (*Cricetus cricetus*) and hare (*Lepus europaeus*); many small birds and mammals also included. (327 prey personally examined, and a similar number by other authors.)

8. *Milvus migrans* (black kite): similar feeding habits to *M. milvus*, but common near water, and fish are an important food item, often obtained from nesting colonies of heron (*Ardea cinerea*) and cormorant (*Phalacrocorax carbo*). The carrion taken also includes most items taken by *Milvus milvus*, but the birds and mammals tend to be of smaller size, e.g. more mice and fewer hamsters.

(126 prey personally examined, and a similar number by other authors.)

Note. Uttendörfer's notes on *Circus* spp. are not nearly so full as for most others.

9. *Circus pygargus* (Montagu's harrier): hunts in open, chiefly on heaths and dryer parts of marshes. Voles (*Microtus arvalis*) are commonest prey (34%), which also includes a fair proportion of young skylarks (*Alauda arvensis*), and young of other ground birds. (About 60 prey personally examined and four or five times this number from other sources.)

10. *Circus cyaneus* (hen harrier): hunts in open, chiefly on moorland, also cornfields; not usually found breeding alongside *C. pygargus*, but habitat difference not adequately analysed. Main food is the vole *Microtus arvalis*, also ground birds and young birds as for *Circus pygargus*. (About 50 prey personally examined, and about five times this number from other sources.)

11. *Circus aeruginosus* (marsh harrier): hunts primarily on marshes, on marsh birds and mammals, these often tending to be of somewhat larger size than the chief preys of the other two species of *Circus*. However, the vole *Microtus arvalis* is often an important item in the diet, sometimes the commonest prey. (About 70 prey personally examined, and about three times this number from other sources.)

12. *Pernis apivorus* (honey buzzard): feeds in woods, primarily on the contents of nests of *Vespa* and other social Hymenoptera. (24 nests studied.)

13. *Pandion haliaetus* (osprey): feeds almost exclusively on fish, usually freshwater, sometimes marine. (Several nests visited, and 60 stomach analyses cited.)

14. *Circaetus gallicus* (snake eagle): a woodland bird, feeding primarily on snakes. (General observations and statements, under 100 prey specified.)

15. *Aquila pomarina* (lesser spotted eagle): frequents wooded country with adjoining marshland, and feeds primarily on frogs, the diet also including small reptiles, mainly lizards and blindworms, and at times the vole *Microtus arvalis*, and insects. (18 nests watched personally, others quoted, and 69 stomach analyses.)

16. *Aquila chrysaëtus* (golden eagle): at present time chiefly in mountain country, feeding mainly on common and arctic hare (*Lepus* spp.), and on grouse and ptarmigan (*Lagopus* spp.). (About 200 prey quoted.)

17. *Haliaeëtus albicilla* (white-tailed eagle): chiefly hunts over water. Main foods: coot (*Fulica atra*) 24%; mallard (*Anas platyrhyncha*) 13%; great crested grebe (*Podiceps cristatus*) 12%; pike (*Esox lucius*) 6%; roe deer (*Capreolus capreolus*) 6%; heron (*Ardea cinerea*) 5%; hare (*Lepus europaeus*) 5%. (412 prey identified.)

B. Strigiformes

18. *Asio otus* (long-eared owl): nests and roosts mainly in woods, feeds partly in woods but commonly in adjacent open country. Main foods: the vole *Microtus arvalis* 78%; wood-mouse (*Apodemus sylvaticus*) (with a very small proportion of related species) 8%. (Based on 50,827 vertebrate prey in pellets.)

19. *Asio flammeus* (short-eared owl): lives in open, on marshes and moorland, primarily on the vole *Microtus arvalis* 97%. (Based on 2148 vertebrate prey in pellets.)

20. *Strix aluco* (tawny owl): nests and roosts mainly in woods, hunts mainly in woods but also in open country on wood edge. Main foods: the vole *Microtus arvalis* 39%; wood-mouse (*Apodemus sylvaticus*) (with small proportion of related species) 14%; bank vole (*Clethrionomys glareolus*) 5%. Many insects also taken. (Based on 38,889 vertebrate prey in pellets.)

21. *Athene noctua* (little owl): lives in open wooded country. Of the mammals in the diet, 76% are the vole *Microtus arvalis*, but this takes no account of the large number of insects, which includes particularly dusk-flying coleoptera. (Based on 1805 vertebrate prey in pellets.)

22. *Aegolius funereus* (Tengmalm's owl): a scarce bird of the mountain forests. Food insufficiently analysed, but the shrew (*Sorex*), and voles and mice of the genera *Clethrionomys* and *Apodemus* appear to predominate. (224 vertebrate prey examined personally, and rather over 400 quoted from other authors.)

23. *Glaucidium passerinum* (pygmy owl): another scarce species of the mountain forests, and food insufficiently analysed. Differs from last in hunting mainly by day, not night. Shrew (*Sorex*), voles and mice (*Microtus*, *Clethrionomys* and *Apodemus*), and small birds (especially titmice, *Parus* spp.) are common in the diet. (Rather over 400 individual prey, cited from other authors.)

24. *Tyto alba* (barn owl): chiefly hunts in cultivated land, over fields and along banks and hedgerows. Main foods: the vole *Microtus arvalis* 51%; shrew (*Sorex*) 19%; house-mouse (*Mus musculus*) and wood-mouse (*Apodemus sylvaticus*) together 14%, in the proportion of about two of the former to every one of the latter. (Based on 36,548 vertebrate prey in pellets.)

25. *Bubo bubo* (eagle owl): often in wooded but also in wild open country. Main foods: the vole *Microtus arvalis* 22%; hare (*Lepus europaeus*) 7%; frog (*Rana*) 6%; water vole (*Arvicola scherman*) 5%; the vole *Microtus nivalis* 5%; partridge (*Perdix perdix*) 5%. (4450 prey examined.)

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THE WILD CAT (*FELIS SILVESTRIS*) IN GREAT BRITAIN

By W. L. TAYLOR, *Forestry Commission*

(With 1 Map in the Text)

The British wild cat (*Felis silvestris*) is the sole surviving representative of the Felidae now to be claimed as native to Britain. The species was formerly widespread in this country and throughout the forested regions of Central Europe, where it continues to retain an extensive geographical range, although it has become extinct in many of its earlier haunts. The wild cat was finally exterminated in England and Wales about the middle of the nineteenth century, the final dates being uncertain owing to doubts regarding the truly feral origin of some of the specimens last recorded as having been destroyed. At approximately the same period wild cats also disappeared from the south of Scotland. Thus in Great Britain, for something like a hundred years, the known habitat of the species has been limited to parts of the Highlands of Scotland. Remarkably little attention has, however, been given to the natural history and geographical range of this most interesting member of the British fauna, and it may be that both numbers and distribution have been greater within the Highland region than naturalists have recognized. In recent years the wild cat has certainly increased its range as well as its numbers in northern Scotland, although none has been recorded elsewhere in Great Britain.

The 1914–18 war provided an opportunity for this wild British animal to improve its status in its last remaining habitat by giving respite from the activities of game preservation, and, to a notable extent, the advantage gained appears to have been held in spite of the fact that these animals are rather easy to trap.

Authorities are generally agreed that the wild cat is untameable; it may rightly be classed as the fiercest animal still to be found wild in Great Britain. Its food is chiefly the flesh of the smaller animals and birds. In appearance it is not unlike the domestic tabby but, owing to its thicker and longer fur, it has the appearance of a more compact and altogether more powerful animal, an impression that is supported by its rather stouter skeletal structure. Recently examined Scottish skins are greyish brown in colour, with black (or almost black) markings, tails being characteristically ringed with black rings and having black tips, blunt and rather bushy, not tapered as in domestic cats. Other distinctive anatomical details are recorded by zoologists, including the fact that the entire length of the intestinal canal of the wild cat is not much more than half that of its domesticated cousin. G. S. Miller (1912), in his *Catalogue of Mammals of Western Europe*, separated the British species from the typical European form as *Felis silvestris grampia*, basing his distinction on the darker coloration and well-defined stripes on the sides and legs of the former.

Authorities give the weight of the wild cat as:

Males 7·25–12·5 lb. (7·25 lb. is described as exceptionally low.)

Females 6·25–10·25 lb.

R. I. Pocock, writing in 1934, refers to a record Scottish specimen weighing 15 lb. 10 oz.

Advantage has this year (1946) been taken of the Forestry Commission's territorial organization to collect information concerning the present range and status of this little-known member of our native fauna, regarding which it is to be hoped that it will not again be harried to a point approaching extinction. The writer is greatly indebted to Mr A. H. Gosling, the Commission's Director of Forestry for Scotland, and to the forest officers and foresters in his Directorate, to whose helpful co-operation the material for the following table is due.

Distribution of the British wild cat

Forest	County	The wild cat is			The numbers are		
		Resident	Occasional	Not known	Increasing	Static	Decreasing
	North						
1. Achnashellach	Ross and Cromarty	×	.	.	.	×	.
2. Ardross	Ross and Cromarty	×	.	.	.	×	.
Borgie	Sutherland	.	.	×	.	.	.
Culloden and Assich	Inverness	.	.	×	.	.	.
3. Clunes	Inverness	×	.	.	.	×	.
Portclair Craignanium	Inverness	.	.	.	.	.	.
Craig Phadrig and Hessock	Inverness	.	.	×	.	.	.
Dornoch and Balblair	Sutherland	.	.	×	.	.	.
4. Eilanreach	Inverness	.	×	.	.	×	.
Findon	Ross	.	.	.	.	.	.

Map 1. Known distribution of the wild cat in 1946 on Forestry Commission areas. Numbers refer to forests.

Distribution of the British wild cat (continued)

	Forest	County	The wild cat is			The numbers are		
			Resident	Occasional	Not known	Increasing	Static	Decreasing
5.	Fiunary	Argyll	×	.	.	×	.	.
	Glenbrittle	Inverness	.	.	×	.	.	.
6.	Glenloy	Inverness	.	×	.	.	×	.
7.	Glenhurich	Argyll	×	.	.	.	×	.
8.	South Laggan	Inverness	.	×	.	.	.	×
9.	Glenrigh	Inverness	.	×	.	.	.	×
10.	Glenshiel, Inverinate, Ratagan	Ross and Cromarty	×	.	.	.	×	.
11.	Glenurquhart	Inverness	×	.	.	×	.	.
12.	Guisachan	Inverness	×	.	.	×	.	.
13.	Inchnacardoch	Inverness	.	×	.	.	.	×
14.	Kilcoy	Ross and Cromarty	.	×	.	.	.	×
15.	Lael	Ross	×	.	.	.	×	.
16.	Leanachan	Inverness	.	×	.	×	.	.
	Longart	Ross	.	.	×	.	.	.
	Millbuie	Ross and Cromarty	.	.	×	.	.	.
	Nevis	Inverness	.	.	×	.	.	.
	Salen	Argyll	.	.	×	.	.	.
17.	Slattadale	Ross	.	×	.	.	×	.
18.	North and South Strome	Ross	× *	.	.	.	×	.
19.	Strathnairn	Inverness	.	×	.	.	×	.
20.	Strathdearn	Inverness	.	×	.	.	×	.
21.	Strathconon	Ross	×	.	.	×	.	.
		East						
22.	Allean	Perthshire	×	.	.	×	.	.
23.	Alltcailleach	Aberdeen	×	.	.	.	.	×
	Bin	Aberdeen	.	.	×	.	.	.
	Blackcraig	Perth	.	.	×	.	.	.
	Blairadam	Fife	.	.	×	.	.	.
	Carden	Fife	.	.	×	.	.	.
	Clashindarroch	Aberdeen	.	.	×	.	.	.
24.	Craigvinean	Perth	.	×	.	.	×	.
	Culbin	Moray	.	.	×	.	.	.
	Deer	Aberdeen	.	.	×	.	.	.
25.	Drummond Hill	Perth	×	.	.	×	.	.
	Drumtochty	Kincardineshire	.	.	×	.	.	.
	Durris and Blackhall	Kincardineshire	.	.	×	.	.	.
	Edensmuir	Fife	.	.	×	.	.	.
	Edens (Pitmedden)	Perth, Fife	.	.	×	.	.	.
	Ferness	Nairn	.	.	×	.	.	.
	Fetteresso	Kincardineshire	.	.	×	.	.	.
	Inglismaldie	Kincardineshire	.	.	×	.	.	.
26.	Inshriach	Inverness	.	×	.	.	.	×
	Keillour	Perth	.	.	×	.	.	.
	Kemnay	Aberdeen	.	.	×	.	.	.
	Kinfauns	Perth	.	.	×	.	.	.
	Kirkhill	Aberdeen	.	.	×	.	.	.
	Lossie	Moray	.	.	×	.	.	.
	Midmar	Aberdeen	.	.	.	.	.	.
27.	Monaughty	Moray	.	×	.	.	×	.
	Montreathmont	Angus	.	.	×	.	.	.
	Newton Nursery	Moray	.	.	×	.	.	.
	Newtyle	Moray	.	.	×	.	.	.
	Ordieguish	Moray	.	.	×	.	.	.
	Pitfichie	Aberdeen	.	.	×	.	.	.
28.	Queens	Inverness	.	×	.	.	.	×
	Roseisle	Moray	.	.	×	.	.	.
29.	Rosarie	Banff	.	×	.	×	.	.
30.	Scootmore	Moray	×	.	.	.	×	.

* Roaming over a fairly wide area.

Distribution of the British wild cat (continued)

	Forest	County	The wild cat is			The numbers are		
			Resident	Occasional	Not known	Increasing	Static	Decreasing
31.	Speymouth	Moray	.	.	×†	.	.	.
32.	Strathord	Perth	.	×	.	.	.	×
	Teindland	Moray	.	.	×	.	.	.
	Tentsmuir	Fife	.	.	×	.	.	.
	Tillyfourie	Aberdeen	.	.	×	.	.	.
			West					
	Achaglachgach	Argyll	.	.	×	.	.	.
33.	Ardgartan	Argyll	×	.	.	×‡	.	.
34.	Asknish, Minard, Strone	Argyll	×	.	.	×§	.	.
35.	Barcaldine	Argyll	×	.	.	×	.	.
36.	Benmore	Argyll	×	.	.	.	.	×
	Benmore Island	Argyll	.	.	×	.	.	.
	Carradale and Saddell	Argyll	.	.	×	.	.	.
	Carron Valley	Stirling	.	.	×	.	.	.
	Devilla	Fife and Clackmannan	.	.	×	.	.	.
37.	Fearnoch	Argyll	.	×	.	.	×	.
38.	Glenbranter	Argyll	×	.	.	×	.	.
39.	Glenduror	Argyll	×	.	.	.	×	.
40.	Glenfinart	Argyll	.	×	.	.	×	.
41.	Inverinan	Argyll	.	×	.	.	×	.
42.	Inverliever and Eridine	Argyll	×	.	.	.	×	.
43.	Knapdale	Argyll	×	.	.	.	.	×
	Lennox	Stirling	.	.	×	.	.	.
44.	Loch Ard	Perth	×‖	.	.	.	×	.
	Loch Ard (Achray)	Perth	.	×	.	.	×	.
45.	Strathyre	Perth	.	×	.	.	×	.
	Tulliallan	Fife	.	.	×	.	.	.
			South					
	Cairn Edward (Bennan)	Kirkcudbright	.	.	×	.	.	.
	Cairn Edward (c)	Kirkcudbright	.	.	×	.	.	.
	Elibank	Peebles	.	.	×	.	.	.
	Garcrogo and Corriedoo	Kirkcudbright	.	.	×	.	.	.
	Changue	Ayrshire	.	.	×	.	.	
	Dalbeattie	Kirkcudbright	.	.	×	.	.	.
	Dundeugh	Kirkcudbright	.	.	×	.	.	.
	Edgarhope	Berwick	.	.	×	.	.	.
	Fleet	Kirkcudbright	.	.	×	.	.	.
	Forest of Ae	Dumfries	.	.	×	.	.	.
	Glentress	Peebles	.	.	×	.	.	.
	Geskine and Auchenrodden	Dumfries	.	.	×	.	.	.
	Kilsture	Wigtown	.	.	×	.	.	.
	Kirroughtree	Kirkcudbright	.	.	×	.	.	.
	Laurieston	Kirkcudbright	.	.	×	.	.	.
	Mabie	Kirkcudbright	.	.	×	.	.	.
	Newcastleton	Roxburgh	.	.	×	.	.	.
	Twiglees and Castle O'er	Dumfries	.	.	×	.	.	.
	Wauchope	Roxburgh	.	.	×	.	.	.

† May possibly be an occasional visitor but unknown generally.
‡ Increasing during past few years.
§ Increasing since 1936.
‖ Regular for past 4 years.

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THE HOUSE-MOUSE (*MUS MUSCULUS*) IN CORN RICKS

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(With Plates 3 and 4 and 3 Figures in the Text)

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1. INTRODUCTION

In Great Britain house-mice are only found abundantly in buildings and in corn ricks. More or less diffused populations are known to live in the fields on islands round the coast (Elton, 1934), and data given in this paper show for the first time that they also live and breed in such habitats inland. Corn ricks are temporary and this necessitates a bridge for the interval: occupying the open fields forms such a bridge. Yet numbers never seem to be great, and there is no evidence that a large population permanently inhabits the fields or exhibits periodic mass increases, such as occur in Australia, California or Russia (Elton, 1942).

This ecological status fits well with the scheme of evolution and spread of the forms of *Mus musculus* L. suggested by Schwarz & Schwarz (1943). Briefly, their suggestion is that most of the forms of house-mouse in the world, with the exception of those in northern and central Europe, have been derived from the subspecies *M. musculus wagneri*, which originally inhabited central Asia east of the Volga. From this area *wagneri* has spread mainly by human aid in two chief directions, (1) south and east reaching from the Riu-kius to South Africa and (2) westwards to North Africa and western Europe including the British Isles, being carried thence to the New World and Australia. The original form of *wagneri*, like the other subspecies, lived in steppes or even deserts and is characterized by having light underparts and a comparatively short tail. As the form has spread it has developed commensal forms, living for the most part with man, and in all the areas concerned characteristic morphological changes have appeared independently, a general darkening of colour and lengthening of the tail. As a rule those 'forms' with the darkest pelage and the longest tails, such as *tytleri* and *castaneus* in India and the Far East and *domesticus* in western Europe, are the most completely confined to buildings, while other forms that have not changed so much are at an intermediate stage of commensalism. It is interesting to find that the British form, cited as one of the most extreme examples of commensalism, does breed quite freely in the fields during the time of year when ricks are scarce.

A comparison of ecological conditions and habits of house-mice in different parts of the world is useful in showing how far the former modify the latter. Information, however, is not very detailed.

In the U.S.S.R. house-mice are on the whole not as commensal as in Britain. They become more completely confined to buildings towards the north (Kuznetzov, 1944), while in the more southern areas most populations are composed of Schwarz's intermediate grade of commensals (apart from the area containing originally wild-living *wagneri*) with only slight morphological modifications. In the

summer most of these forms live mainly in the fields, especially weed-grown areas and banks of gullies (Fenyuk, 1941). One particular form, the hillock-mouse, *M. musculus hortulanus*, is described as living in the Ukraine (Naumov, 1940) in hillocks which it builds and where sufficient food is stored for the winter. In normal circumstances, therefore, this form does not need the shelter of stacks and houses. Other forms generally move in towards the villages about November and concentrate, sometimes in large numbers, in field margins, heaps of weeds, ricks and houses. Many also live in burrows in the ground.

Mortality at this season is evidently very high, as shown by the experiments of Kalabukhov & Raevskii (1933), in which they ringed large numbers of mice and recovered the rings in the castings of hawks and owls. Census techniques also show the same rapid decline (Fenyuk, 1941), and it is clear that dense cover is most important for the wild-living house-mouse (compare this with the comparatively low numbers trapped in the fields after threshing given in the present paper, p. 144).

Survival during the winter is therefore, as in Britain, largely in houses and stacks, except on some steppe areas. As to stacks, most mice are found in unthreshed ricks (e.g. 18 per cu.m. in unthreshed and 2 per cu.m. in threshed millet according to Fenyuk, 1941), but the high numbers that are, nevertheless, found in straw and hay stacks show that cover is of greater importance than in Britain. This also is in the face of great competition with other species, chiefly voles, which is unknown in this country. We have found that the only other abundant inhabitant of corn ricks was the brown rat (*Rattus norvegicus* Erxl.), while bank voles (*Clethrionomys glareolus* Schreber) were occasionally seen. Venables & Leslie (1942) mention as well the wood-mouse (*Apodemus sylvaticus* (L.)), and, rarely, the harvest-mouse (*Micromys minutus* Pallas).

For other countries there is little information as to the normal status of feral house-mice except in years of mass increase. In the United States conditions are evidently not dissimilar to Britain: most small mammal surveys include a few house-mice, and Linduska (1942) found it the third commonest species in winter shocks of maize.

There is a considerable amount of literature on mass outbreaks, however. Most of this is summarized by Elton (1942). In the U.S.S.R. such outbreaks in the regions east and west of the Volga are not uncommon, and descriptions of the course of two have been given by Fenyuk (1934, 1941); there are also details in Kalabukhov & Raevskii (1933). The latter, investigating the populations of straw stacks in the northern Caucasus, found remarkable densities of the order of 75 per cu.m. This was at the beginning of the winter, when the rate of invasion from the fields was at its height. Afterwards figures dropped rapidly, showing that these stacks were used largely for cover and the mice foraged outside them.

Similarly in Australia very large densities are recorded at intervals, though here enormous numbers may be living in the fields and migrate into buildings when the food supply has been eaten out. The climatic factor is probably not so important as in Russia. In 'plague' years densities of burrows in the fields may reach 10,000–24,000 per acre (Anon. 1917).

In California there was an outbreak on a similar scale (for details see Hall, 1927) in 1926. The interesting point about these mass outbreaks is that in two of the areas (Australia and California) the mice concerned would be of Schwarz's most highly developed commensal type, whereas in the U.S.S.R. they would be much more of the free-living type. It appears that a propensity to mass outbreaks is not correlated with the type of mouse concerned. In the case of the Russian outbreaks, Kalabukhov (1937) advances evidence to show that the main cause of these is fluctuation in the main species of food plant. Similarly in the case of the hillock-mouse, whose numbers fluctuate within smaller limits, large numbers moving about the country are correlated with dry autumns, when there has been little growth of the weeds, whose fruits supply the staple food.

In Britain there are said to be years when mice are particularly abundant on farms, but there is nothing approaching the dimensions of these mass outbreaks. On the other hand, owing to the ecological conditions (density of corn ricks and lack of really hard weather) there are violent oscillations in populations of a seasonal character. Corn ricks in this country are built in August and September and most are threshed by April of the following year. There is therefore a mass of house-mice released into the fields during autumn and winter, the great majority of which must be quickly eliminated by predators (see figures for field trapping on p. 144). British house-mouse populations exhibit remarkable self-regulation through these periods of alternating light and heavy mortality, and the mechanism of this regulation presents a problem of great interest in fundamental ecology.

This paper does not pretend to do more than substantiate and elaborate two main facts related to this problem. The first is that these temporary rick populations are very large and are widely and homogeneously spread over the arable parts of the country. The second is that field populations are largest in summer, when sparse colonies live and breed in and around the cornfields, whence they invade or are carried into the new ricks.

For rick populations to remain at this generally

high level one must assume that these sparse colonies of the summer, when few or no ricks remain, never suffer sufficient mortality to prevent an evenly spread invasion of the new ricks, nor remain abundant enough for the rick populations to soar wildly. The constant rise and fall of numbers suggests a nicely adjusted mechanism, whose critical point is somewhere during the summer. An intensive study of this period would be interesting.

2. THE SIZE OF CORN-RICK POPULATIONS

Few other habitats can provide conditions so favourable to rapid increase of house-mice as a corn rick (see reproductive rates given on p. 145 from Laurie, 1946). There is cover for evading predators and for minimizing intraspecific strife; abundant food for maintaining health and reproduction; shelter from storms, wet and cold (Venables, 1942–3 (unpublished), showed that a corn rick in winter can have a mean temperature 2–8° F. higher than outside); and an almost complete relaxation of the commoner causes of mortality. These factors lead to the building up of very large populations in a very short time.

Venables & Leslie (1942) classify mouse infestations of corn ricks in categories, of which the highest is 'over 200'. These were adequate for their purpose, but give no critical estimate of maximum populations. During 1943 a number of ricks were carefully investigated by us and fairly complete counts of the total populations made at threshing. The following method was used.

As soon as the thatch was removed the straw from this was piled up into one or two heaps a little distance from the rick and the ground around it cleared of vegetation. When large samples of corpses were required for examination, a roll of string netting with $\frac{1}{4}$ in. mesh was hung over the wire netting, with which each rick is surrounded. During the threshing of the top part of the rick practically all mice that dropped to the ground ran into the base of the rick again or into one of the straw heaps. Occasional ones which escaped were counted. In the meantime as many of the mice as possible were killed by hand to avoid confusion in counting when the base of the rick was reached. Even so, counting became difficult towards the end and two observers were usually employed during this time. Finally, the base of the rick was turned over and the number of mice there counted: similarly with the straw heap 'refuges'.

In Table 1, which shows the total numbers of mice in all corn ricks examined, nos. 1–32 were estimated in the way described above. Nos. 33–40 were ricks in which all the mice had been killed by gassing with carbon dioxide. During this process the whole rick was covered with gas-proof fabric, which was sealed into a trench at the base of the rick. Up to 79% of the population was picked up outside the rick when the cover was removed; the rest were obtained during threshing.

From Table 1 it can be seen that the total population of badly infested ricks varies widely. The figures given for mice per cu.m. are more satisfactory than totals, because rick size is variable. Even here the figure varies from 1·39 to 14·0. Part of this variation will obviously be due to the different stages of growth of the populations and this factor is considered next.

3. GROWTH OF HOUSE-MOUSE POPULATIONS DURING THE YEAR

This can be traced in two ways: first, by comparing figures for density of mice generally at different months of the year, and secondly, by tracing the course of infestations in a single rick.

Table 1 gives some information on the first point, but it must be remembered that these ricks were chosen as examples of bad infestations (these were the most suitable for work on control, which was going on at the same time). This table, therefore, really only gives an approximation to the maximum numbers. Even so, it may be seen that during spring and summer the mean density in badly infested ricks in their first year of age is somewhat higher than in the winter, and the two remarkably high densities occur during the spring and summer.

Further data on this subject are available from a country-wide survey of mice and rats in ricks conducted by C. Elton & Laurie (unpublished) from 1943 to 1946. These were sent in by threshing-tackle foremen from 19 to 25 areas (representing 12–14 counties) in England from January to March and, in smaller numbers as the ricks decreased, from April to June. Combined figures for wheat, oats and barley ricks over the four years concerned are given in Table 2.

These figures show that the proportion of infested ricks and of ricks with heavy infestations (over 50 mice) is increasing sharply at the beginning of the year. After this the number of ricks infested remains fairly steady, suggesting that there is not much infestation of new ricks (indeed, there are few left to infest): however, the number of heavy infestations continues to rise slightly. None of these data includes the first months after a rick is built which would show how the populations are built up. However, Venables & Leslie (1942) have a table showing the distribution of house-mouse populations in formal (estimated) categories of density for 4-week periods beginning on 20 Aug. Their data for 1940–1 with subsequent corrections provided for the writers by

Table 1. *Total populations of house-mice in corn ricks selected as examples of bad infestations*, 1942–5

Note. Nos. 17–34 and 37 give figures for which a considerable degree of accuracy is claimed. The others were not estimated so precisely and probably err on the low side. Nos. 8–16 composed a group of small ricks evenly infested. An average figure for one of them is given.

In the column headed 'Corn' O = oats, W = wheat and B = barley.

In the column headed 'Season' the figure given is the number of seasons for which the rick has been standing, i.e. a second season rick is over 12 months old.

'Active' mice include all those from about 5 g. in weight. Smaller mice are usually in the nest or just crawling about outside it.

No.	Locality	Corn	Season	Threshed	Size cu.m.	'Active' mice	All mice	Active mice/ cu.m.	All mice/ cu.m.	Rats, etc.
				1942						
1	Wootton, Oxfordshire	O	2	15–16 Dec.	68	*c.* 800	—	11·76	—	23
2	Do.	O	1	17 Dec.	57	> 200	—	> 3·51	—	21
3	Do.	O	1	19 Dec.	57	> 300	—	> 5·26	—	0
4	Do.	O	1	21 Dec.	57	*c.* 200	—	3·51	—	20
5	Do.	O	1	22 Dec.	57	*c.* 150	—	2·63	—	20
6	Do.	O	1	23 Dec.	57	*c.* 250	—	4·39	—	51
				1943						
7	Do.	O	2	4 Jan.	68	*c.* 800	—	11·76	—	—
8–16	Do.	O	2	8–10 Jan.	39	> 200	—	> 5·01	—	—
17	Do.	W	1	13 Jan.	60	> 300	—	> 5·01	—	—
18	Do.	O	2	14 Jan.	97	> 1000	—	> 10·31	—	—
19	Begbroke, Oxf.	B	1	2 Apr.	83	300	—	3·60	—	—
20	Do.	B	1	3 Apr.	83	204	—	2·40	—	—
21	Sutton, Oxf.	W	1	21 Apr.	71	935	996	13·31	14·00	7
22	Do.	O	1	7 May	60	292	345	4·87	5·75	0
23	Do.	O	1	7–8 May	60	330	353	5·50	5·88	2
24	Cote, Oxf.	W	1	20–21 May	126	653	952	5·18	7·56	2
25	Do.	W	1	21, 22, 25 May	126	782	1041	6·21	8·26	0
26	Kirtlington, Oxf.	W	1	31 May, 1 June	138	766	1033	5·55	7·49	3 yg stoats
27	Begbroke, Oxf.	W	1	11–12 June	158	1996	2368	12·63	14·99	6
28	Cote, Oxf.	W	1	15–16 July	111	872	—	7·86	—	12 (+6 yg)
29	Botley, Oxf.	W	1	29 July	82	424	483	5·17	5·89	6
30	Do.	W	1	30 July	82	215	268	2·62	3·27	26
31	Northleach, Gloucestershire	O	2	24–25 Nov.	123	386	—	3·14	—	2; 2 weasels
32	Do.	O	2	26, 29–30 Nov.	123	483	529	3·93	4·30	3 (+1 yg)
				1945						
33	Nr. Morpeth, Northumberland	W	2	12 Apr.	77	260	294	3·38	3·82	0
34	Do.	W	2	13 Apr.	84	—	111	—	1·42	0
35	Do.	W	2	14 Apr.	73	206	—	2·82	—	0
36	Do.	W	2	16 Apr.	70	70	—	1·00	—	0
37	Chipping Norton, Oxf.	W	1	22 June	46	114	—	2·48	—	2
38	Do.	W	1	23 June	36	50	—	1·39	—	1
39	Do.	W	1	23 June	36	100	—	2·78	—	0
40	Finmere, Oxf.	O	1	10 Aug.	176	250	—	1·42	—	—

Table 2. *Degree of house-mouse infestation in corn ricks from January to June in representative English areas (April to June figures for 3 years only)*

Month	No. of ricks	No. infested	Percentage	No. with over 50 mice	Percentage
Jan.	1409	1179	83·7	608	43·2
Feb.	1453	1326	91·3	767	52·8
Mar.	1454	1337	92·0	788	54·2
Apr.	724	671	92·7	394	54·4
May	508	468	92·1	314	61·8
June	177	167	94·4	107	60·5

Mr Leslie are shown in Table 3. This table shows the very rapid way in which infestations spread, especially as the figures apply to whole rick groups and not merely to ricks standing close to each other between which mice might be expected to pass rapidly.

A further analysis of the material in Venables & Leslie's table shows also the increase in size of the populations month by month. Of the categories used, those from 3–5 represent rick groups with populations of 50 mice and upwards, so that if the sum of groups 3–5 is expressed as a percentage of the total, a figure comparable to those from Elton & Laurie's survey is obtained, and the latter are extended by observations right from the beginning of the season (20 Aug.), though from a limited area round Oxford.

piling up at the foot of the rick (see Pl. 3, photo 1). In spite of this it seems that most ricks will reach a maximum density when 8–11 months old and do not increase greatly beyond this point. Figures from Table 1 may be summarized as shown in Table 5. These figures are small, but there is no suggestion that density is positively correlated with the age of the rick after 8 months.

Certain of these data, together with others collected by one of us (E. M. O. L.), carry the analysis a stage further by allowing the effect of the type of rick to be separately assessed.

Figures from Table 6 (ricks 41–63) have been kept for separate treatment because they give information about a random sample of ricks instead of their being chosen (as in Table 1) for abundant traces of mouse occupation. Most of the ricks in Table 6 were used

Table 3. *Decline in proportion of uninfested ricks from August to April, Oxford District*, 1940–1

	20 Aug.–16 Sept.	17 Sept.–14 Oct.	15 Oct.–11 Nov.	12 Nov.–9 Dec.	10 Dec.–7 Jan.	8 Jan.–4 Feb.	5 Feb.–4 Mar.	5 Mar.–1 Apr.
No. of rick groups	14	23	24	17	16	14	21	18
No. *without* mice	14	16	11	6	3	2	3	1
Do. %	100	70	46	35	19	14	14	6

Table 4. *Rise in proportion of ricks with 50 house-mice and over from August to April, Oxford District*, 1940–1

	20 Aug.–16 Sept.	17 Sept.–14 Oct.	15 Oct.–11 Nov.	12 Nov.–9 Dec.	10 Dec.–7 Jan.	8 Jan.–4 Feb.	5 Feb.–4 Mar.	5 Mar.–1 Apr.
No. of rick groups	14	23	24	17	16	14	21	18
No. with 50 mice and over	0	3	6	2	6	9	10	8
Do. %	0	13	25	12	35	64	48	44

Table 5. *Density of house-mice in first and second season ricks*

	No. of ricks aged	
Active mice/cu.m.	8–11 months	11 months and over
2·0–5·9	6	5
6·0–9·9	2	0
10·0+	2	3

The figures here for spring populations are of the same order as those obtained from the country-wide survey, but the rapid way in which numbers are built up in autumn and early winter is emphasized. By December about a third of the ricks are populated by over 50 mice, and by January this proportion has increased to about a half.

Ricks left unthreshed into the second year after building are not commonly found, but, since we were seeking badly infested ricks, a number were discovered. They appeared to be in a state of extreme dilapidation with chaff oozing out from all sides and

in an attempt to correlate the number of mouse runs on the outside with density of the population (see pp. 139–43) and were chosen right at the beginning of the season, when traces were scanty and it was not known whether a dense population would develop. Thus the figures for density are nearly all considerably below those in Table 1, and Tables 1 and 6 are to some extent complementary.

In Fig. 1 density is plotted against the age of the rick, and the results show a low density to start with and a rise in average during spring and summer with the highest figures occurring only at these seasons.

However, if the figures for wheat ricks alone are considered, a much more coherent picture of increase is obtained. From a mean density of about 0·1 mice per cu.m. in February, there is an increase to about 0·5 in March and to about 2·5 by May. This is an increase in 3 months of about 25 times in the mean density.

Possibly, therefore, house-mice find a more satisfactory environment in wheat than in other kinds of ricks. At any rate it is clear that the usual report by

farmers of house-mice doing most damage in oat ricks is not justified by these figures. The impression is doubtless fostered by the greater length of time for which some oat ricks are left standing.

From this comparison it can be seen, even if the last 3 months are disregarded owing to the small number of oat ricks threshed, that infestations are at once commoner and larger in wheat than in oat ricks.

The second method of tracing the increase of house-mouse populations in corn ricks is by devising an index to the numbers, which can be applied periodically to the same rick. With this idea in mind a number of ricks in the Oxford District were chosen during 1943 and 1944 and counts were made just before threshing of the number of mouse-holes in the sides of the ricks up to a height of 6 ft., so that this figure could be compared with the total of 'active' mice found at threshing. During the early stages of an infestation these holes are not very easy to trace, but careful examination reveals small pieces of nibbled grain and a gradual accumulation of chaff at the entrance to the holes. After some months, when a medium-sized infestation has been built up, signs are much easier to see (Pl. 3, photo 2), and in an old rick the difficulty is to decide where one hole ends and another begins (Pl. 4).

The figures for these ricks are given in Table 6. Here the density of the holes is expressed as the mean number per sq.m. of the rick surface searched. All

Table 6. *Density of house-mouse runs, or holes, in rick sides compared with density of mice, Oxford District*

Note. In ricks 41–63 the actual total of mice was known only within the approximate limits indicated. The mean of these limits has been taken for calculating the density per cu.m.

All ricks in this table were in their first season except nos. 30 and 31.

In the column headed 'Corn' O = oats, W = wheat and B = barley.

No.	Corn	Date threshed	No. holes per sq.m.	No. mice	No. rats	No. mice per cu.m.
		1943				
24	W	20–21 May	6·75	653	2	5·18
25	W	21, 22, 25 May	7·4	782	0	6·21
26	W	31 May, 1 June	7·9	766	0	5·55
27	W	11–12 June	9·2	1996	6	12·63
28	W	15–16 July	10·3	872	12	7·86
29	W	29 July	4·7	424	6	5·17
30	W	30 July	4·1	215	26	2·62
31	O	24–25 Nov.	8·9	386	2	3·14
32	O	26, 29, 30 Nov.	8·9	483	3	3·93
		1944				
41	B and O	19–22 Feb.	6·45	50– 75 (63)	1	0·40
42	B and O	23 Feb.	5·8	50– 65 (58)	0	0·39
43	B and O	25 Feb.	3·3	75–100 (83)	0	1·41
44	B	7 Feb.	1·3	15– 20 (18)	0	0·18
45	B	18 Mar.	3·6	25– 30 (28)	0	0·25
46	W	7 Feb.	0·6	*c.* 5	0	0·04
47	W	14 Feb.	1·6	35– 40 (38)	0	0·21
48	W	15 Feb.	1·2	25– 30 (28)	0	0·14
49	W	16 Mar.	2·4	60– 70 (65)	0	0·76
50	W	17 Mar.	1·65	50– 75 (63)	2	0·42
51	W	17 Mar.	1·7	40– 50 (45)	0	0·32
52	W	23 Mar.	2·2	80–100 (90)	0	0·64
53	W	28 Apr.	3·15	300–400 (350)	0	3·53
54	W	2 May	3·8	*c.* 300	0	2·10
55	W	3 May	1·9	250–300 (275)	0	2·32
56	O	24 May	2·3	50	0	0·81
57	O	25 May	4·05	50	0	0·81
58	O	26 May	6·0	50	4	0·81
59	O	16 June	3·3	*c.* 30	0	0·25
60	W	5 June	2·3	250–300 (275)	0	2·04
61	W	15 June	3·6	400–500 (450)	0	3·00
62	O	25–26 Aug.	3·8	*c.* 20	6	0·18
63	O	26–27 Aug.	1·7	*c.* 20	0	0·18

four sides were counted up to about head level, leaving out only a strip of 1–3 ft. in width up to the eaves. In addition, Table 6 contains nine ricks from those in Table 1, in which the hole density was taken from the number of poison baits placed in the rick. These figures are equivalent, since baiting was done in the holes only. Since these were ricks with large populations, they extend the range of the other figures.

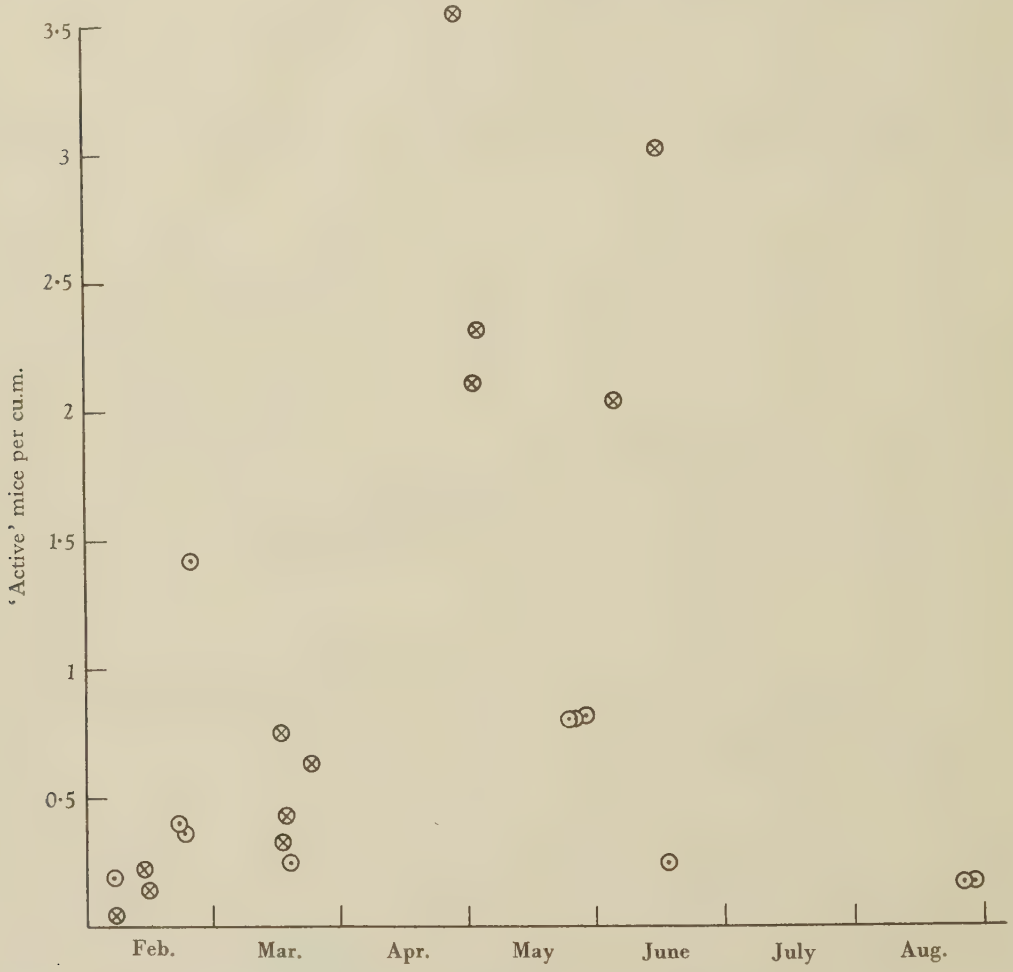

Fig. 1. Density of house-mice compared with age of rick in random sample of ⊗ wheat, ⊙ barley and/or oat ricks.

The results can be seen best in Fig. 2. In oat and barley ricks there is no constant relation between the number of holes and the number of mice, so that these figures must be discarded for the present purpose. The trouble arises from the less closely packed nature of an oat or barley rick compared with a wheat rick and from the less rigid straw. This means that the mice have less well-defined runways and push out chaff and kibbled grain at many points on the surface instead of at discrete holes only. With wheat there is a fairly well-marked tendency for the number of holes to increase with the number of mice. Generally speaking this relation is constantly proportional, the density of holes per sq.m. being always slightly greater than the density of mice per cu.m. This relationship must be accepted with considerable reserve because of the wide scatter and paucity of the points on the graph, but within these limits the relation is marked enough to suggest that most of the mice in a stack visit the outside surface. If this were not so, one would expect the density of mice to increase faster than that of the holes, in fact in somewhat the same ratio as exists between increases in volume and surface area. This confirms results obtained by poison baiting (see p. 147).

Referring back to Table 1, we see that the maximum density of mice in a sample of badly

infested ricks may increase in 4–6 months by just under 200% (maximum density in December 5·26 per cu.m.; in April 13·31 per cu.m.).

Finally Venables & Leslie suggest from analysis of their data that an increase in 6 months of the order of 350% may take place.

In view of these figures a special series of hole counts was made during the seasons 1943–4 and 1945–6 at wheat ricks in the Oxford neighbourhood. The full results are given in Table 7 and are summarized in Fig. 3. Ricks 1–3 were investigated in 1943–4 and the rest in 1945–6, and it is evident that

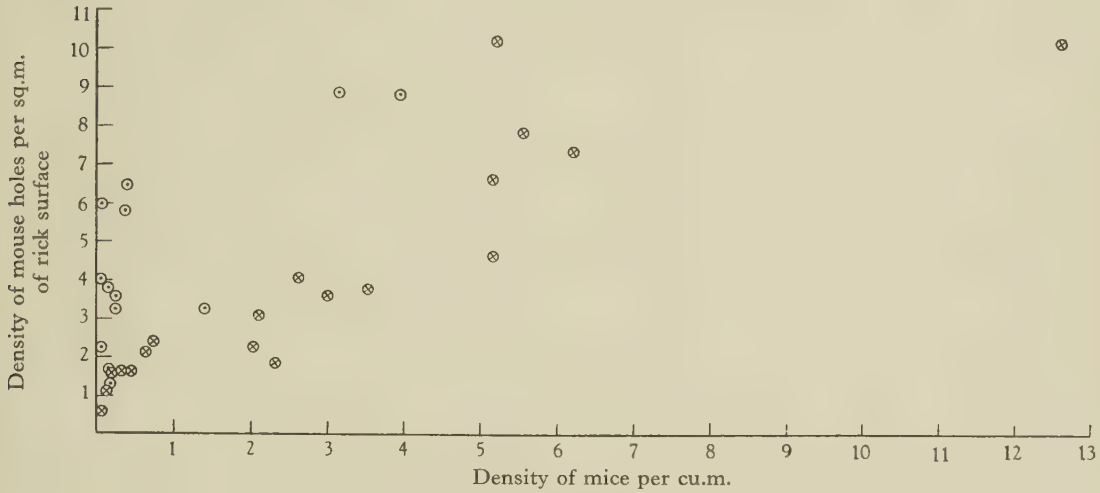

Fig. 2. Relation between densities of mice and of mouse holes in ⊗ wheat, ⊙ barley and/or oat ricks.

Table 7. *Counts of house-mouse holes in the sides of wheat ricks in the Oxford District done at intervals throughout the season*

The figures italicised represent the density of holes per sq.m. of rick surface searched (this varied between 30 and 60 sq.m.).

	First count				Second count				Third count		
Rick no.	Date	Holes	Holes/ sq.m.	Gap (days)	Date	Holes	Holes/ sq.m.	Gap (days)	Date	Holes	Holes/ sq.m.
1	21 Dec.	46	*1·3*	118	18 Apr.	93	*2·6*	—	—	—	—
2	29 Feb.	68	*1·4*	47	17 Apr.	132	*2·75*	—	—	—	—
3	29 Feb.	68	*1·4*	47	17 Apr.	107	*2·2*	—	—	—	—
4	17 Nov.	17	*0·3*	61	22 Jan.	32	*0·6*	—	—	—	—
5	17 Nov.	12	*0·4*	61	22 Jan.	18	*0·5*	—	—	—	—
6	17 Nov.	10	*0·3*	61	22 Jan.	26	*0·6*	—	—	—	—
7	27 Nov.	6	*0·2*	62	28 Jan.	11	*0·3*	42	11 Mar.	20	*0·6*
8	27 Nov.	1	*0·02*	62	28 Jan.	8	*0·2*	42	11 Mar.	16	*0·4*
9	28 Jan.	5	*0·1*	42	11 Mar.	18	*0·4*	51	1 May	48	*1·0*
10	28 Jan.	13	*0·3*	42	11 Mar.	30	*0·7*	36	16 Apr.	38	*0·8*
11	26 Nov.	4	*0·07*	50	14 Jan.	6	*0·1*	42	28 Feb.	20	*0·4*
12	26 Nov.	4	*0·07*	50	14 Jan.	8	*0·1*	42	28 Feb.	14	*0·2*

					Fourth count				Fifth count		
				Gap (days)	Date	Holes	Holes/ sq.m.	Gap (days)	Date	Holes	Holes/ sq.m.
7	—	—	—	36	16 Apr.	24	*0·8*	—	—	—	—
8	—	—	—	36	16 Apr.	25	*0·6*	—	—	—	—
9	—	—	—	—	—	—	—	—	—	—	—
10	—	—	—	—	—	—	—	—	—	—	—
11	—	—	—	33	2 Apr.	48	*0·9*	41	13 May	58	*1·0*
12	—	—	—	33	2 Apr.	22	*0·3*	41	13 May	25	*0·4*

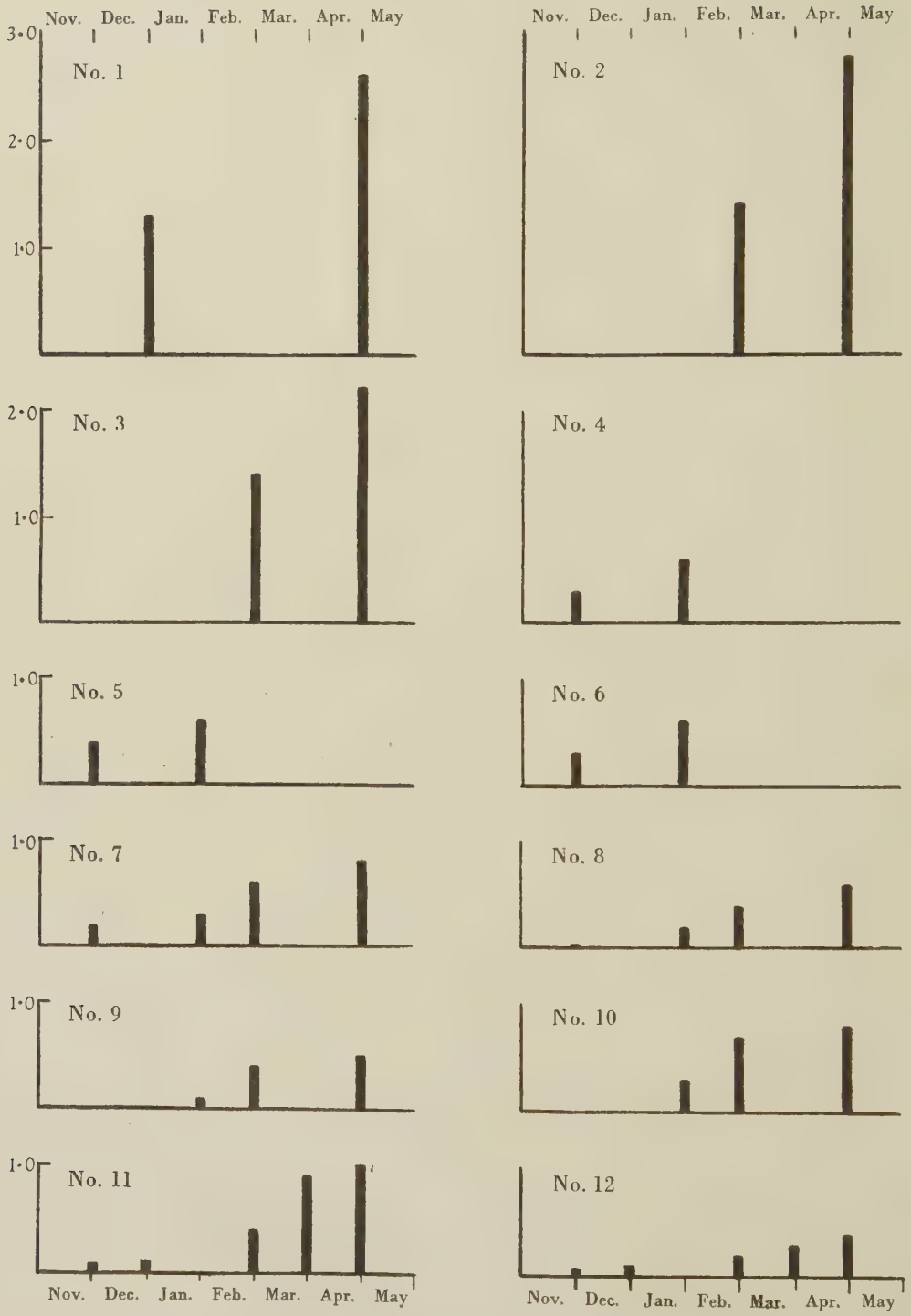

Fig. 3. Increase through the season in density of house-mouse holes in the sides of individual wheat ricks. Ordinate = no. of holes per sq.m. of rick surface examined. For full details, see Table 7.

the degree of mouse infestation was higher in the former year. This, however, may only have been due to variation in the areas from which the samples were drawn. In all cases except nos. 1 and 5 there was an increase of 100% or over during the period through which counts were made, and the larger figures become apparent early in the new year: after this there is some variation, for instance, nos. 2 and 11 show a continuing sharp increase into May, while others, such as nos. 7, 8, 9, 10 and 12 may stay about the same after February or only rise at a fairly slow speed. The reason for this difference is obscure, since the environment of a corn rick would seem to provide conditions in which the rate of increase would be stable, but no doubt there are various factors which have not been evaluated.

Fig. 3 shows that in the early months the rate of increase may be as much as 300% per month (no. 9), but the more general rate is of the order of 100% (nos. 7, 8 and 10) per month. This, however, is not maintained over many months: for instance, nos. 4 and 6 show an increase of about 50% per month over 2 months. In the later months there is similar variation, but generally the rate is lower. No. 11 shows an increase from February–March to March–April of 100%, but this is an isolated instance, the more usual progress being such as is shown by nos. 2 and 3 or even by nos. 7, 8, 9, 10 and 12 (less than 25% per month).

If these figures are a reflection of the density of mice, we may say that, disregarding the very small initial figures of some of the ricks, populations will about double themselves every 2 months.

These estimates from different sources are in rough agreement and show that the problem of house-mice in ricks is a serious one economically. A population that will double itself in 2 months, treble itself in 4 months and more than quadruple itself in 6 months is obviously approaching conditions for maximum reproductive efficiency indicated by Laurie (1946).

A point of considerable importance is that only a very small initial population is necessary to produce a heavy spring and summer infestation. This means that the handful of mice that may be carried into the rick when it is built are quite enough to cause heavy damage if the rick is left unthreshed.

4. BREEDING SEASON AND ALTERNATION OF HABITAT

In a corn rick breeding would be expected to go on at a steady rate at all seasons. By examining over 8000 mice from all kinds of environments one of us (Laurie, 1946) has shown that breeding is remarkably constant in the three main environments occupied by mice in this country (corn ricks, food stores and general 'urban' premises), and that there is no particular breeding season. In corn ricks, however, the rate of breeding is consistently higher than in the other two environments; an adult female mouse in a corn rick has 10·2 litters per year compared with the figure of 5·5 for 'urban' mice. This figure approaches closely to the calculated maximum number of litters that a mouse can produce in a year, which is 13–14, so that this is some measure of the satisfactoriness of conditions in a rick. Practically this figure only operates for part of the year, so that rick mice have a breeding 'season' coincident with the life of their rick. On the other hand, mice living in the fields (see later) seem to have only a summer breeding season.

The number of corn ricks in the country is reduced to a minimum between April and September, so that it is important to discover what happens to house-mice in the country between these months. As mentioned before (see §1) the house-mouse is partly or wholly a field animal in some other parts of the world: for Britain practically no data existed on this point. Accordingly, a field trapping campaign was carried out to throw some light upon this problem. Apart from a preliminary trial in August 1943, trapping was all carried out in the Oxford district between June 1944 and June 1945. The main objects in view were to find out (*a*) whether house-mice live out in the fields and hedgebanks all the year, (*b*) whether they have a breeding season, and (*c*) what is their range and distribution in relation to farm buildings and ricks.

The trapping was all done with break-back traps baited with rolled oats and staked to the ground when necessary. If this was not done, traps set along the hedgerows in the winter often disappeared. Traps were set in lines at intervals of 3–4 ft., and, when placed in growing corn, the lines were parallel to and about 3–6 ft. from the edge of the crop.

(*a*) *Numbers of house-mice caught by field trapping*

The total number of house-mice caught during the 12 months was 128 in 6855 trap nights (details in Table 9).

The commonest field inhabitant is usually the wood-mouse (*Apodemus sylvaticus*) with the bank vole (*Clethrionomys glareolus*) coming second in order. From Table 8 it is seen that catches of house-mice were not far below those of the bank vole, while they were just under half of the wood-mouse total and far ahead of any of the less common species. This means that, taking the figures over the whole year, the house-mouse is the third commonest small mammal living on this English arable land: a rather remarkable result, when it is considered that previously the evidence that it lived in the fields at all was slight. On the other hand, it was only to be

Table 8. *Totals and percentages of small mammals caught in* 6855 *trap nights, Oxford District*

	Mus musculus	*Apodemus sylvaticus*	*Clethrionomys glareolus*	Other small mammals	Total
Total	128	290	152	47	617
%	20·6	47·0	24·6	7·8	100

Table 9. *Distribution of all house-mice caught in traps according to time of year and habitat*

Date	Standing corn	Stooks	Corn rick	Straw rick	Hedges nr. rick	Hedges	Stubble	Total	Trap nights	No. per 100 trap nights (by months)
15–19 June	4	—	—	—	—	—	—	4	250	0·9
24–29 June	1	—	—	—	—	—	—	1	300	
17–20 July	0	—	—	—	—	—	—	0	72	
17–20 July	0	—	—	—	—	—	—	0	52	
20–21 July	3	—	—	—	—	—	—	3	70	0·6
20–23 July	0	—	—	—	—	—	—	0	96	
21–23 July	0	—	—	—	—	—	—	0	93	
25–31 July	0	—	—	1	—	—	—	1	301	
30 July–8 Aug.	—	0	—	—	—	—	—	0	288	
31 July–2 Aug.	8	—	—	—	—	—	—	8	174	
4– 9 Aug.	14	—	—	0	—	—	—	14	344	2·9
4–10 Aug.	—	1	—	—	—	—	—	1	306	
12–25 Aug.	31	—	1	0	—	—	—	32	730	
19–24 Aug.	—	4	—	—	—	—	—	4	172	
23–28 Sept.	—	—	8	—	6	—	—	14	95	14·7
29 Sept.–2 Oct.	—	—	—	—	1	0	—	1	95	
3– 7 Oct.	—	—	0	—	—	0	0	0	220	
11–16 Oct.	—	—	4	—	—	5	0	9	438	2·2
18–24 Oct.	—	—	0	—	—	1	0	1	344	
25 Oct.–1 Nov.	—	—	1	9	5	7	0	22	404	
16–23 Nov.	—	—	1	0	4	—	0	5	411	1·2
4– 7 Dec.	—	—	0	—	—	0	—	0	152	0·9
16–19 Dec.	—	—	0	3	0	0	0	3	200	
18–21 Jan.	—	—	1	—	—	1	—	2	126	1·6
6– 9 Feb.	—	—	0	—	1	—	0	1	163	0·3
20–23 Feb.	—	—	0	0	0	0	—	0	170	
13–17 Mar.	—	—	0	—	—	0	—	0	220	0·3
22–25 Mar.	—	—	—	—	1	0	0	1	176	
5–12 June	—	—	—	—	—	1	—	1	270	0·3
13–15 June	—	—	—	—	—	0	—	0	123	
Total	61	5	16	13	18	15	0	128	6855	
%	47·5	3·9	12·5	10·2	14·2	11·7	0	100		

Table 10. *Variation of catch of small mammals according to locality, Oxford District*

Locality	Description	*Mus musculus* Total	*Mus musculus* %	*Apodemus sylvaticus* Total	*Apodemus sylvaticus* %	*Clethrionomys glareolus* Total	*Clethrionomys glareolus* %	Other small mammals Total	Other small mammals %	Total	Trap nights
Compton, Berkshire	Arable on chalk downland	8	29	19	68	0	0	1	3	28	908
Botley, Berkshire	Arable near woodland	5	4	74	66	20	18	13	12	112	786
Freeland, Oxfordshire	Arable	14	32	4	9	22	50	4	9	44	344
Begbroke, Oxfordshire	Arable near houses	31	20	96	63	23	15	3	2	153	1640
Hampton Poyle, Oxfordshire	Arable	70	25	102	36	87	30	26	9	285	3177

expected in view of the habits of the species in other countries. The results of Linduska (1942), who investigated the small mammal populations of winter shocks of maize in Michigan, are interesting to compare. He found that house-mice, as in England, were the third commonest species, representing 12, 13 and 24% of the catch in three fields.

(*b*) *Variation according to locality*

All the trapping was carried out on agricultural land in the Oxford neighbourhood with a large proportion of arable ground. Results analysed by localities (Table 10) show individual variation in the percentage of house-mice caught. This may be partly due to variation in the numbers of mice in neighbouring ricks, though equally the latter will depend on the numbers of free-living mice to enter them. It is, in fact, very difficult to determine the role of corn ricks in maintaining field populations of house-mice. The latter occur as far away from ricks or rick sites as possible in arable areas, and furthermore a high pregnancy rate was discovered in the sample examined (see later). Nevertheless, the variations of density from place to place are difficult to explain on a long-term view except by variability in the winter cover provided by ricks.

(*c*) *Variation according to habitat*

To some extent this is bound up with seasonal variation, but the main point to determine under this heading is whether there is any suggestion that field populations of mice are, on a short-term view, dependent on artificial cover such as corn or straw ricks, and whether they are distributed with such artificial cover as focal points. Table 9 shows that, leaving aside entirely the summer populations which are found in standing corn and under stooks, about equal numbers of mice were caught around ricks and along hedgerows (29 and 33): further, that of the latter figures more than half (18) were caught fairly near to ricks. There is therefore a definite tendency for populations to centre round ricks and rick sites, though most intervening ground may be occupied by fair numbers. The catching of house-mice right out in the hedges during the winter suggests that there need be no short-term (e.g. daily) movement back to rick cover, and that they are perfectly capable of living in hedgerow cover in the severest weather. It is noteworthy, however, that mice were never caught in the open fields until the corn had grown up. In this way their habits are similar to those observed in the U.S.S.R. (Fenyuk, 1941).

Table 11 gives the distribution of all house-mice caught around ricks and in the hedgerows (apart from those trapped in standing corn) according to the distance from ricks at which they were trapped.

Table 11. *Distribution of field-living house-mice according to distance from rick cover*

Distance from nearest rick (yd.)	No. mice caught	Distance from nearest rick (yd.)	No. mice caught
0–	9	100–	5
10–	13	150–	3
20–	7	200–	1
40–	0	250–	9
60–	0	300–350	6
80–	2	Total	55

It is immediately clear that there is a gap between mice caught quite close to a rick and those caught some distance away. This suggests that all the latter at least were living away in the hedgerows quite independently of any artificial cover, and further, that up to a fifth of a mile away the population is still substantial. This does not mean that the presence or absence of rick cover will not affect the *general* density of house-mice in the neighbourhood concerned.

(*d*) *Variation according to season*

Table 9 shows that during the summer mice may be caught in some numbers in standing corn and under stooks, but few are found round the straw ricks (hedgerows were not trapped at this season). In the autumn fair numbers are found round the new ricks and out in the hedgerows up to at least 350 yd. away from rick sites. Later still in the year and in the early spring considerably smaller numbers are found mainly in the hedgerows, but not out in the open fields. At the two localities, which contribute most of the evidence from September onwards, no threshing was done after December, so that it seems certain that the few mice caught from January onwards had maintained themselves in hedgerows only. It is possible that the winter under consideration (1944–5) was particularly severe upon these field populations, and normally a larger number may be able to survive until the late spring, when they can move to the growing corn. There is clearly no tendency in the figures for these mice to move back to the neighbourhood of straw stacks during wintry weather.

(*e*) *Pregnancy and fecundity*

A total of 64 house-mice was caught between June and August 1944, of which 34 females and 28 males were identifiable. Of the males 68% were fecund and of the females 94%. Of the fecund females 40% (13/32) were pregnant. This rate is almost exactly the same as the average rate found for female mice in corn ricks during the year (see Laurie, 1946), and is higher than the rate in other habitats. From September 1944 to March 1945 56 house-mice were

caught, of which 16 females and 40 males were identifiable. Of the males 77·5 % and of the females 75 % were fecund, but only one of the latter, trapped at the end of September, was pregnant. Although the winter figures are small, the disproportion in the pregnancy rates is marked, and it is clear that very little breeding occurs during autumn and winter outside the ricks. A similar disproportion is seen in the sex ratio, showing that males rather than females tend to winter outside the ricks.

In the U.S.S.R. it has been shown that, except in ricks, breeding is at a minimum in winter, though quite a large number of pregnancies occur in autumn (Kalabukhov, 1937; Fenyuk, 1937).

The following general conclusions may be drawn in view of these field trapping results:

(1) After harvest some mice are found in the new ricks, where their numbers begin to increase slowly at first. Other mice live around the ricks and in the nearby hedgerows, but among these breeding is at a minimum.

(2) During the autumn mice are found both around the ricks and at considerable distances away along the hedgerows. The latter probably live quite independently in the fields: breeding is still at a minimum. Meanwhile their numbers are being augmented by a trickle that survives from threshing.

(3) In winter numbers outside the rick decrease. This tendency may have been exaggerated in the localities studied by early threshing of most of the ricks and by severe weather. Trapping shows a thin population still in the hedgerows with even less caught round the ricks. There is little or no breeding except in the ricks, where the populations are beginning to be large.

(4) In spring the situation is still much the same. Where threshing continues, however, large numbers of mice are now turned loose and the survivors spread into the fields. Trapping results are meagre for this season, but those for the summer show this effect.

(5) By summer quite large populations are living in standing corn and breeding at about the same rate as rick populations. The biggest catches were in localities where late threshing had turned out large numbers of mice, but in other places mice were not infrequently caught, so that increase from hedgerow and cornfield breeding evidently takes place.

(6) When the corn is cut, some mice remain in the stooks, in which presumably they get carried into the ricks. Others doubtless remain in the hedgerows, though the trapping results are not very clear on this point.

The main differences between the habits of mice in Britain and the U.S.S.R. are that with us the bulk of the breeding occurs in ricks, and, although summer breeding occurs in the fields at a high rate, the population is too small for vast numbers to be built up outside rick cover.

5. MOVEMENTS AND DISTRIBUTION OF HOUSE-MICE WITHIN RICKS

Once mice have entered a rick they rarely move out until the rick is threshed. We have frequently watched mice running about the sides of ricks, but no instance has occurred of one being seen to move away from the rick. In fact, when mice fall from the rick sides, which often occurs as the result of a scuffle, they are always observed to run straight into the base of the same rick.

Unlike rats, mice do not need to forage outside a rick for water; in captivity they live in good health on a diet of wheat, which itself contains about 15 % of water, though they will take a small amount more if it is provided. This is generally less than 1 ml. per day, and this quantity would be easily obtained on the outside of the rick in the form of dew or rain. Probably this accounts for most mice in a rick visiting the outside, and for the readiness with which they take poison bait mixed with water.

In an infested rick there are generally a number of main runways in the base, through which mice re-enter, if they fall off, and through which new mice can enter. The main part of the population, however, is higher up. An instructive observation was made at a rick near Stanton Harcourt, Oxfordshire. A 2-year-old linseed rick had no traces of mice on the outside, but, since it had been cut in two for half to be threshed, a cross-section was exposed. This showed that most of the rick was too densely packed for mice to get in, but in a few places, where several layers of stems were placed together or weeds had been included, thus spoiling the tightness of the packing, mice had found a way in and nests and runways had been constructed.

Sixteen ricks were carefully examined for the distribution of house-mice in them, and out of this number nine were most damaged in the middle and higher parts (mid-stem, high-stem and top). Very few of them were not badly infested in the top, and the one case, where this did not hold good, this part was composed of another strain of corn mixed with a multitude of thistles. Six of the ricks had especially heavy damage at the edges, which confirms the suggestion made above that mice tend to settle round the outsides first. This is also confirmed by the fact that it is possible to detect even a very small population (5–30) by traces in the form of runs, chaff, kibbled grain and droppings on the outside of the rick. Of course, since most of these ricks were chosen for the large size of the infestations, most of the preference for any particular part of the rick will have been obscured by the pressure of a rapidly

Photo H. N. Southern

Photo 1. Rick 17 (Table 1). Piles of chaff at the base of the rick.

Photo H. N. Southern

Photo 2. Rick 17 (Table 1). Chaff accumulations at the mouth of runs in the side of the rick.

Photo H. N. Southern

Rick 17 (Table 1). End of rick showing damage and general dilapidation caused by *Mus musculus*.

growing population. The statement by Venables & Leslie that mice tend to occupy the lower part of a rick is accounted for (as the writers indeed suggest) by their ricks having also large rat populations.

The range of movement of mice in a corn rick is fairly extensive. The appearance of the mouse runs in the side of a rick with the entrance almost choked up with chaff and kibbled grain suggests that such debris is cleared out of the run from the inner part of the rick. Also the variation in outside activity between a fine, warm day and a cold, wet one is so marked that obviously movement to the outside is of regular occurrence. Evidence on this point was gathered during poison-baiting trials using zinc phosphide. In the first place the fact that generally over 70% and occasionally over 90% of the mice could be killed with baits pushed about 12 in. into the runs is proof that a large amount of movement

Table 12. *Ratio of poisoned house-mice picked up outside ricks*

Weather	Total corpses found	% found outside
Fine	196	18·5
Fine	288	8·0
Cold east wind	139	13·5
Cold east wind	156	10·0
Fine	451	14·5
Fine and warm	1373	23·0
Fine and warm	380	19·5
Fine and warm	343	5·5
Very cold; exposed position	339	0·0

to the outside takes place. This is probably not so much as the rates of killing suggest, because mice may carry the bait into the rick for considerable distances. This is especially noticed when a rick has been overbaited, for pieces are commonly found 2–3 ft. inside the rick, while more scattered pieces occur further in and occasionally some are lying right in the middle. The same distribution is observed in the corpses of mice poisoned, though more are found in the middle than is the case with the baits.

Experiments to determine the range of house-mice living under 'domestic' conditions were carried out at Oxford, and these showed that, although the mean range was fairly small (*c.* 50 sq.ft.), this was not further compressed by increase of density. Instead the range was shared. Therefore even in a corn rick, where the density is much greater than in these experiments, the range must be something of this order, extending in most cases to the outside of the rick. Additional evidence of this centrifugal movement is provided by the proportions of poisoned mice found outside ricks before threshing (see Table 12). These figures show the notable variation, generally but not always correlated with the weather, of activity on the outside of a rick. In addition to this evidence one may add the interesting ratio of runway to population density discussed on pp. 139–43.

Vertical movement within a rick is not so marked as lateral. In many poison tests it was not possible to bait the roof of a rick. In all these cases very few corpses were found in the roof and the main bulk of them started fairly suddenly at a clearly defined level. This was very marked in a preliminary trial, in which a band of baits was put into the sides of the rick at about head-level: most of the dead mice were found about this level when the rick was threshed.

6. RATE OF DAMAGE TO THE GRAIN

This is extremely difficult to assess. The impression gained from examining the sheaves in a badly infested rick is that there can hardly be any corn left at all, since nothing but piles of chaff and kibblings are to be seen. One cannot entirely neglect the opinion of farmers that mice do more damage in a rick than rats. To place the matter on a basis of measurement is, however, difficult.

A certain amount of damaged grain is lost from the sheaves as they are picked up, especially if there is a high wind. Some of this would otherwise come through with the tail corn, though most would go with the dust, which is not usually measured. The process of threshing separates out the different categories of damage very successfully. First comes the best, or millable, grain, and here there is usually very little damage. A few grains may have been nibbled, but this is not enough to be significant. Secondly comes the tail corn, or tailings, and it is here that the bulk of the damaged grain appears. A certain amount consists of under-sized grains, but the greater part is grain that has been nibbled to an extent of 50% or more. Generally, too, a fair amount of mouse droppings come through with the tail corn. Finally, there is the 'dust', which in a rick free of mice consists of weed seeds and scarcely fills a sack. In a mouse-infested rick, however, there may be several sacks of dust, composed almost wholly of kibblings and of droppings. It is an impressive sight to watch a sack filling up almost entirely with mouse droppings, and it emphasizes the scale of the infestation much in the same way as when one of the writers weighed a sack of poisoned mice from one rick and found there was nearly 28 lb. of them.

The actual separation of the categories varies with the setting of the sifting mechanism in the threshing machine. If the farmer wants a good sample of millable corn he may have the adjustment set so that only the largest grains come in the millable, while the tailings consist of the smaller and damaged grain. Conversely, if he wants to reduce the percentage of

tail corn (this will often happen in a damaged rick, since with wartime controls a farmer was liable to be suspected of inefficiency if the tailings constituted more than 5 % of the yield), he will have the setting shifted in the other direction. Such variation is obvious when yields are compared with the known mouse populations (see Table 13).

It is difficult to get satisfactory figures for the actual loss in weight due to mice, since these must be based on estimates of the probable yield of a rick, if not infested. The alternative of having comparable ricks threshed at different times of the year is better, but no actual instances have been checked by the writers, and there are only reports from farmers upon which to rely. The following may be mentioned as examples.

Four large oat ricks near Northleach, Gloucestershire, had been built at harvest time in 1942 and of these two were threshed in September 1943, and two in late November 1943. The kind of oats (White Victor) was one which was grown every year here and the usual yield per rick for an average crop was about 130 sacks. Thus the four ricks should have given about 520 sacks; in fact they gave 410, a deficit of 110 sacks, or 21 % of the estimated yield.

Of two oat ricks at Hampstead Norris, Berkshire, comparable in every way, one was threshed in the October after it was built and yielded 107 sacks of millable corn and 4 of tailings; the other was left until the following July and gave 99 sacks of millable and 14 sacks of tail corn. The deficit in gross weight for the latter rick is 16 cwt. (7 sacks) or 6·4 % of the previous yield.

This estimate is undoubtedly more accurate than the first one because the only factors imperfectly known are the amount of damage done to the first rick by October, and the number of rats concerned.

The figures can be roughly tested in another way. A house-mouse eats on the average 3·4 g. of wheat a day (Southern, unpublished data). In a month the consumption would be 102 g. or just over 3·5 oz. and in 9 months about 2 lb. In this period the rick quoted lost a total of 16 cwt. or 1793 lb., a loss which would be equivalent to a population of nearly 900 mice living in the rick for the 9 months.

This shows that the figure of 16 cwt. given is probably on the high side, since a population equivalent to 900 mice all the time would have to build up to a very large total. Therefore, although the amount is by no means impossible, it is likely that there was some other factor, e.g. rats, influencing the loss.

The percentage of tail corn, though subject to the variation already indicated on pp. 147–8, may be taken as a very rough guide to the degree of infestation by mice, as shown in Table 13. In the ricks cited above we know that a level of 12 % tailings is equivalent to a loss in actual weight of about 6 %, though this must only be taken as the merest approximation.

Table 13. *Percentage of tail corn in house-mouse-infested ricks, Oxford District*

In the column headed 'Corn' O = oats, W = wheat and B = barley.

Locality	Corn	Date threshed	No. of house-mice	Yield (in sacks)		
				Millable	Tailings	Tailings, %
Begbroke (2 ricks)	B	14 and 18 Mar.	*c.* 30 in each	180	10	5·5
Yarnton (9 ricks)	W	Mar.	*c.* 50 in each	422	4·4	0·96
Begbroke (3 ricks)	W	15–17 Mar.	*c.* 60 in each	170	6	3·5
Hampton Poyle	B and O	25 Feb.	75–100	12·5	1	8·0
Kirtlington	W	3 May	250–300	64	2	3·1
Cassington	W	3–5 June	250–300	45	1·5	3·3
Kirtlington	W	1–2 May	300	70	3	4·3
Sutton	O	8 May	331	59	4	6·4
Botley	W	29 July	424	65	2	2·7
Cote	W	15–16 July	800	50	6·5	13·0
Sutton	W	21 Apr.	996	20	4	16·6

It should not be forgotten that damage to grain is not the only loss incurred in a rick through mice. The straw is often so mangled that it cannot be built into a rick, but has to be baled or chopped up for feeding to cattle. Furthermore, a rick which is full of dust and in which most of the sheaves have their binding twine bitten through takes a great deal longer to thresh with consequent increase of expenditure on labour and fuel.

7. SUMMARY

1. In Great Britain the house-mouse (*Mus musculus* L.) lives mainly in corn ricks and buildings. Populations in country areas alternate seasonally between a high density, while the corn ricks are occupied, and a low density of mice living in the fields when all ricks have been threshed, though there are a few mice living in the fields at all seasons.

2. Figures on population density from the Oxford neighbourhood show that badly infested ricks may

contain from 1·4 to 14 mice per cu.m. These populations show a rapid rate of occupation of ricks in the autumn, and by January over 90% of ricks are infested. The size of population rises rapidly in the early months after the ricks have been built, reaching a peak in the spring; after a rick is 8 months old there is little if any increase in the mouse population, however long it may stand.

3. Counts of mouse-holes in the sides of ricks show that in wheat there is a fairly constant relation between the number of holes and the number of mice. Oat and barley ricks are presumably too loose for any such relation to be established. Counts of holes in wheat ricks through the season show roughly the rate of increase in size of the population.

4. Break-back trapping in and around cornfields proved that the house-mouse is the third commonest small mammal living in the fields. After harvest the mice are found around ricks and in the hedgerows nearby, but by autumn they are caught at considerable distances away from rick cover and are obviously living independently of it. During winter the field populations are small, but by spring, possibly increased by large numbers released from ricks at threshing, more of them are found in the cornfields. They have now started to breed at quite a high rate. By the summer this field population is more than sufficient to reinfest the new ricks as they are built.

5. Though house-mice rarely come out of corn ricks once they have settled in, their range within the rick is considerable and most of the population visits the external surface of the rick, as proved by poison-baiting experiments in the sides of the rick, which sometimes killed 90% of the population.

6. The amount of damage done by house-mice in corn ricks is difficult to evaluate exactly, but it is shown that, within very approximate limits, an index of this damage is given by the percentage of tailed corn in the total yield at threshing.

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THE INTERSPECIFIC RELATIONS OF ANTS

By DEREK WRAGGE MORLEY

1. INTRODUCTION

The Formicidae are among the most widely distributed of all the animals, ranging from near the Arctic Circle and high up on the mountains to the Tropics and deserts; indeed, Zschökke has termed them 'eurythermal ubiquists' on this account.

There are few regions in the world where man has far to search before he finds some ants. They may not be obvious before he starts to search, although often their presence is only too evident: they may be under the bark of trees, in the thorns of shrubs, or living a troglodytic existence under the surface of the earth, but they are nearly always there and of more than one species. Only in the coldest months of the year are they inactive and difficult to find.

This biological success of the ants is reflected in the large numbers of species of other insects (myrmecophiles) described as being found only in their nests: over 1200 myrmecophiles have so far been described. All these insects obtain some benefit from their association with the ants, whether it be food or protection, or whether they be parasites or true guests. This is in part only an inverse reflection of two further factors: (1) The highly developed social life of the ants, which makes their dominance where they occur more effective than that of the non-social species of insects. (2) The interspecific competition amongst the ants themselves.

Forel (1928) has said that 'the chief enemy of an ant is another ant': that is perhaps an overstatement of the case, but one which contains, nevertheless, a very large measure of truth. The combination of these two factors renders the study of the interspecific relations of ants one of especial interest both to ecologists and to students of animal behaviour. The various interspecific relationships of ants have, of course, been studied in considerable detail by many myrmecologists, most notably Wheeler, Forel and Wasmann. That aspect of the subject which concerns the occurrence of mixed and compound colonies of ants, where different species of ants live side by side or mixed together (and which the author has recently termed *mixobiosis*)* has received special attention.

Wheeler's classification (1910; see also Wragge Morley, 1945) of the mixobiotic colonies of ants deals, however, only with a part of the interspecific relations of ants and is based on what is fundamentally a purely descriptive character. Let me illustrate this point: Wheeler divides the mixobiotic colonies of ants into two main types—compound nests and mixed nests. In the former the brood of each species is kept separate; in the latter it is not. Thus the mixed-nests category contains mostly obligatory relationships, yet thieving life (lestobiosis), robbing life (cleptobiosis), soldiership (phylacobiosis) and guestship (xenobiosis) are included in the compound nests category because of the essentially photographic basis of the classification. In the same way the competitive or beneficial nature of the various relationships is not stressed. Furthermore it is this same factor which limits the use of Wheeler's systematic approach. It embraces only those relationships which are more or less static and which occur in the nest or its immediate area. An explanation of the picture thus obtained is sought, but the starting point is the photographic picture of the nest.

* I am indebted to Dr Julian Huxley and Dr C. K. Ogden for pointing out to me that my original spelling of this term 'mixtobiosis' was philologically incorrect.

2. CLASSIFICATION OF INTERRELATIONS

It is intended here to try and present briefly a more comprehensive systematic approach to the study of the interspecific relations of ants, in which behaviour is used as the basis for the various groupings. There are two main categories of interspecific relations in ants: those which are facultative or casual, and those which are obligatory. Examples of the former are first, the facultative slave-maker *Formica sanguinea* L., which usually makes slaves of one of three other species of ants, but does not always do so and can exist quite happily without its slaves; secondly, the interterritorial competition between our woodland *Formica rufa* L. and *Acanthomyops fuliginosus* Latr. when they casually occur in the same woodland area. An example of the obligatory type is the case of the obligatory slave-maker *Polyergus rufescens* L., which cannot feed itself and would die unless it were able to make successful slave-making raids on one of two or three slave-species. Each of these cases will be mentioned again later.

These two main categories may be broadly divided into two further classes: tolerant or co-operative relationships, and competitive relationships. The result is as follows:

A. CASUAL AND FACULTATIVE RELATIONSHIPS*

1. *Casual competitive relationships*

(*a*) Preying.
(*b*) Interterritorial competition.

2. *Facultative competitive relationships*

(*a*) Facultative slave-making.

3. *Facultative non-competitive relationships*

(*a*) Originally casual colonial associations (plesiobiosis).
(*b*) Track-sharing (parabiosis).
(*c*) The relations of normally non-competitive species occurring in the same habitat.

B. OBLIGATORY RELATIONSHIPS

1. *Obligatory tolerant or co-operative relationships*

(*a*) Guestship (xenobiosis).
(*b*) Soldiership (phylacobiosis).

2. *Obligatory competitive relationships*

(*a*) *Intra-nidal.*

1. Obligatory slave-making (dulosis).
2. Temporary social parasitism.
3. Permanent social parasitism (colacobiosis).

(*b*) *Extra-nidal.*

1. Thieving (lestobiosis).
2. Robbing (cleptobiosis).

A. CASUAL AND FACULTATIVE RELATIONSHIPS

1. *Casual competitive relationships*

(*a*) *Preying*

One species of ants preys on another species in the course of its predatory activities. This occurs much more frequently than has been generally recognized, especially in the Tropics. Most of the termite-hunting Ponerine ants (for example, *Euponera*, *Lobopelta*) frequently attack the nests of other species of ants which they encounter during their expeditions. The army ants (Dorylinae) are particularly noteworthy in this respect. The preying is, however, casual. Even amongst our own British ants this may be an important factor in interspecific relationships. Ants will often attack the nest of another species in order to obtain the larvae and pupae for food, particularly where the ant fauna is dense and species of ants which form less permanent nests are concerned. It has been suggested (Donisthorpe, 1927) that the slave-making habit may have arisen through the accidental bringing to maturity of pupae taken for food in such raids. This relationship is closely bound up with the next one.

(*b*) *Interterritorial competition*

In any given habitat competition is most marked between those species having similar habits and ecological demands. This can best be illustrated by reference to an actual case, for example, the author's studies of the ant fauna of a garden at Bournemouth (Wragge Morley, 1944). The species present in the garden were: *Acanthomyops niger* L.; *A. fuliginosus*, *A. mixtus* Nyl.; *Formica fusca* L.; *Myrmica rubra* L.; *M. scabrinodis* Nyl.

Both *niger* and *mixtus* formed large polycalic colonies of a permanent nature and there was considerable competition between the two species during the latter part of the eight years, marked by considerable fluctuations of territory boundaries. In such cases one species may eventually drive out the other, but often both seem to survive with constant fluctuations in their success.

There can be no doubt that in the case of these large polycalic colonies interspecific competition is a factor of major importance. Where, however, the species do not compete so directly the relationship may become more static, as with *Acanthomyops fuliginosus* and *Formica rufa*, often found in the same woodland area.

The competition between the species with smaller colonies and less permanent nests is not nearly so great, and, since they are nearly always predatory, is reflected in a fluctuating population in which frequent interspecific preying occurs. Examples of this in the Bournemouth garden were seen in the case of *Myrmica* spp. and *Formica fusca*.

The large polycalic colonies nearly always seem to succeed when opposed to the aggregations of the smaller ones, as occurred in the Bournemouth garden. There is, of course, much intercolony competition among the smaller colonies which is nullified in the case of those species with large polycalic nests.

2. FACULTATIVE COMPETITIVE RELATIONSHIPS

(*a*) *Facultative slave-making*

The slave-maker may exist without slaves, for example, *Formica sanguinea* Latr. Donisthorpe (1927) states that only on two occasions has he found

* It is hoped that the specialized ant-study terms here given in parenthesis will be abandoned as unnecessary. Nearly all the special terms invented to describe ant behaviour are redundant, confusing and deserving of an early death. Often they are used merely to hide the perhaps unwitting ignorance of the writer, and they are nearly always unnecessary. The few used here are included in order to aid their death and to prevent the confusion which their entire abandonment might cause in the minds of some myrmecologists!

nests of *sanguinea* in this country without slaves. Forel (1928), however, records a large polycalic colony consisting of more than forty nests, in which no slaves were present, but in which many of the workers were of unusually small stature. Wasmann (1905), however, records that he found several strong colonies of *sanguinea* in which no slaves were present at Exaten in 1890, 1896, 1897 and 1898, and another in Luxembourg in 1904. According to him (transl.): 'The average proportion of masters and slaves in the most populous colonies is from 100 : 1 to 10 : 1, in the middle-sized and weak colonies, however, from 3 : 1 to 1 : 1...it is plain that the number of slaves in different colonies changes each year and lastly, the number of slaves depends also on special local circumstances. Where slave nests are very numerous, e.g. in groves of birches and oaks, there more slaves will be found in the *sanguinea* nests than on the open heath, where *fusca* nests are very scarce. Yet, *ceteris paribus*, we find the constant law, that in a given *sanguinea* nest, the number of slaves and that of masters is not in *direct* but in *inverse* proportion. My observations of *sanguinea* nests in Dutch Limburg, Rhineland, Vorarlberg, Bohemia and Luxemburg, everywhere confirmed this law.' Although the observations of other workers cast doubt on the existence of quite so exact relationship as Wasmann supposes, there can be no doubt that the *sanguinea* slave-making is of a very different type to that of the obligatory slave-makers, and is correctly termed 'facultative'.

3. *Facultative non-competitive relationships*

These are usually temporary relationships liable to easy upset, especially in times of scarcity or abundance.

(*a*) *Originally casual colonial associations* (*plesiobiosis*)

Where colonies are established close together, usually under the same stone, but remain quite separate from one another. Many such relationships have been observed and the author has recently described a series of such colonies found at Porlock, Somerset (Wragge Morley, 1945). The relationship is undoubtedly due in the first place to the accidental founding of colonies by queens of different species in the same shelter (be it stone or tree trunk). When the colonies become too large fighting occurs and the relationship is broken. In the Porlock colonies fighting occurred in every case when the stone was lifted and the earthen barriers made by the ants were broken down. This fighting was, however, undoubtedly due in part to the excitement and confusion caused by the complete removal of the stone, and not to the breaking down of the barriers alone.

Sometimes, as with our *Myrmica scabrinodis* and *Acanthomyops flavus* F., it may lead to a robbing (cleptobiosis) relationship, but this is unusual and the robber colonies of the *Dolichoderine* scavengers are not founded in this way, being obligatory, not facultative.

(*b*) *Track sharing* (*parabiosis*)

The broods are separate, but the ants use the same 'roads' when going out to forage. Forel (1898) first described this relationship when he found *Crematogaster parabiotica* F. and *Dolichoderus parabiotica* F. living together in this fashion. There seems to be no reason to suppose that the relationship is obligatory. Wheeler (1910) also places here the colonies of different species of ants nesting in the same tree.

(*c*) *The relations of normally non-competitive species occurring in the same habitat*

In the author's paper on the ant fauna of a Bournemouth garden (Wragge Morley, 1944) it is remarked that 'workers of *Formica fusca* and *Myrmica scabrinodis* were observed wandering unharmed on the tracks of the mixed *Acanthomyops fuliginosus* = *Acanthomyops mixtus* colony. Intermingling of foraging workers of *Myrmica scabrinodis* and *Acanthomyops niger*, and *Myrmica ruginodis*, *F. fusca* and *Ac. niger* was also observed.' Elsewhere such interspecific tolerance has frequently been observed. The interspecific tolerance of *Acanthomyops fuliginosus* and *Formica rufa* L. already mentioned does not, however, come into this category since there is no intermingling.

B. Obligatory relationships

1. *Obligatory tolerant or co-operative relationships*

(*a*) *Guestship* (*xenobiosis*)

The guest ant relationship. The nest is compound (i.e. the broods of the two species are kept separate, but the relationship is very intimate). The guest species is never found except in association with the host species. Examples of 'guestship' are the small Myrmicine ants *Leptothorax emersoni* and *L. glacialis* which are found in the nests of species of *Myrmica* in New England and the Rocky Mountains respectively. The brood of guest and host are kept separate, but the small *Leptothorax* build minute passages leading into the larger ones of the *Myrmica*. Through these passages they enter the *Myrmica* nest and mounting the back of one of the *Myrmica* lick her cuticle feverishly: a service which the *Myrmica* seem to accept willingly. In this way the *Leptothorax* both obtains the oleaginous salivary secretion with which the *Myrmica* cover themselves when they clean one another and, as often as not, a drop of food regurgitated from its host's crop. Forel (1928)

states that the *Myrmica* are so attracted by this licking that individuals sometimes break into the *Leptothorax* nest in order to obtain more of it! *L. glacialis* appears to be more parasitic than *L. emersoni*, doing less licking and pomading, and being in every way more helpless. Wheeler managed to persuade the *L. emersoni* to feed normally in captivity after somewhat 'clumsy' first attempts, but it has never been taken apart from its hosts.

Stäger (1925) has shown that the relationship between our own *Formicoxenus nitidulus* and the wood ant *Formica rufa* is similar. Forel (1928) states that the *Formicoxenus* follow their hosts if they migrate.

(*b*) *Soldiership* (*phylacobiosis*)

Two cases of soldiership have been recorded, one by Wasmann (1901–2) who coined the term phylacobiosis, and one by the author (1945) on information obtained and communicated by Dr Julian Huxley. The only known examples are both ant-termite relationships, but 'soldiership' is included here on account of its extraordinary interest. Wasmann found the ant *Camponotus termitarius* in the nest of *Eutermes fulviceps*, where the ants appeared to be playing the part of soldiers in the joint community. No termite soldiers of nasutes were present. In the second case the species of ants and termites are unknown, but there were again no termite soldiers or nasutes present, and the relationship appeared to be the same. The ants were present in each of the half-a-dozen colonies of that species of termite opened by Dr Huxley.

2. *Obligatory competitive relationships*

(*a*) *Intra-nidal*

1. *Obligatory slave-making* (*dulosis*). *Polyergus rufescens* has already been instanced as an example of this category. It is never found apart from its slaves and if kept in captivity without its slaves will die, even if food is present in abundance.

2. *Temporary social parasitism*. In this case the queen of the parasitic species enters the nest of the host species after the nuptial flight in order to found a new colony. She usually kills the queen of the host species (which is usually monogynous) and is accepted in her stead. In a few cases it seems likely that she is accepted while the host queen is still alive. Usually under such circumstances the host queen is killed, but sometimes she appears to be allowed to live, but is not replaced on her death (see Wragge Morley, 1945).

An example of this relationship is that of our *Acanthomyops fuliginosus* Latr. which founds its colonies in the nests of *A. umbratus* Nyl., which in turn may found its colonies in a similar manner in the nests of *A. niger*.

3. *Permanent social parasitism* (*colacobiosis*). Several species of ants are permanent social parasites in the nests of other species of ants. Most of these species, of which there are very few, are not known to possess workers. A good example is our own *Anergates atratulus* (Schenck). This workerless parasite is found in the nests of *Tetramorium caespitum* L. Copulation takes place in the nest and after a nuptial flight the female *Anergates* seek out nearby *Tetramorium* nests. The *Anergates* females are nearly always received in a friendly fashion, although occasionally short battles occur between the female and a few *Tetramorium* workers. Other genera which belong to this group are *Epixenus* and *Anergatides*.

(*b*) *Extra-nidal*

1. *Thieving* (*lestobiosis*). The thief-species of ants are always considerably smaller than the host species with which they live. The nest is compound and the thief ants keep their nest walled off from that of the host species except for the small passages through which they enter and leave the nest of the larger species for their thieving. This relationship differs from guestship (xenobiosis) in that the thieving species offer nothing to the host species in return for their depredations, and the food they steal is not, as with the guest-species, given them willingly by their hosts, but is fugitively stolen. A guestship relationship does not appear to cause harm to the host species, although food is undoubtedly lost through it: a thieving relationship is always harmful to the host species and may seriously handicap the success of its colonies.

Our little *Solenopsis fugax* (Latr.) is a thief ant, living in the nests of *Formica fusca* and many other species and genera.

2. *Robbing* (*cleptobiosis*). Some species of ants, especially some of the Dolichoderinae, build their nests near, although not actually within the precincts of, the nests of other species of ants, and live chiefly by robbing the returning foragers of the 'host' species of their food (usually pieces of insect-flesh or grain).

They also act the part of scavengers of nest refuse and of the battlefield.

The grouping of the interspecific relations of ants given above is logical. Furthermore, their myrmecophilous relationships (other insect-ant relationships) can be dealt with under the same system. It is capable of easy expansion as new relationships are discovered, and it is based on two simple factors: (1) the obligatory, or facultative or casual, nature of the relationship; and (2) whether it is competitive or not. It presents a clearer picture of the factors

involved in the various relationships than Wheeler's earlier 'photographic' classification, and it is hoped that it may prove a useful tool for the more intensive study of this fascinating and important subject.

3. SUMMARY

1. The exceptionally wide distribution of the ants and their highly developed social life, which makes their domination where they occur more effective than that of the non-social species of insects, together with the intense interspecific competition amongst the ants themselves, renders the study of their interspecific relations one of considerable ecological importance. It is also of especial interest to students of animal behaviour.

2. Wheeler's classification of the mixobiotic colonies of ants is criticized on the grounds of its purely descriptive basis and its incompleteness. A more comprehensive systematic classification in which behaviour is used as the basis for the various groupings, is presented.

3. There are two main categories of interspecific relations amongst the ants: those which are casual or facultative, and those which are obligatory. These two main categories are further divided into tolerant or co-operative relationships, and competitive relationships. The result is summarized on p. 151. A description of each type of relationship is given, together with examples illustrating them.

4. Myrmecophilous relationships can be dealt with under the same system, which is capable of easy expansion as new relationships are discovered. An earnest prayer is made for the abandonment of many of the useless and confusing specialized myrmecological terms.

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SALMON OF THE RIVER SHANNON IN 1944 AND 1945

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(With 5 Figures in the Text)

1. INTRODUCTION

(*a*) *The hydro-electric scheme*

In 1929 a radical change took place in the River Shannon as a habitat for salmon as a result of the hydro-electric development of the resources of the river, and within a few years it became obvious that considerable differences were to be observed in the stocks of salmon. Apart from the very obvious diminution in numbers, the character of the salmon had changed. Early running and, therefore, relatively heavy fish, were smaller in number than before the 'Shannon scheme' was initiated; but the late running or summer fish appeared to have suffered little reduction. A problem, therefore, presented itself as to whether the conditions observed from, say, 1935 to 1941, could be regarded as typical, or did they merely represent a transitional stage of rehabilitation of the river to its previous state.

In the year 1941 a new fishing weir, now known as Thomond Weir, was operated for the first time for a full season, and a collection of data and material was made with a view to investigating the life history of the incoming populations of salmon in that year. A report on this investigation has already been published (Went, 1943), and it was then shown that significant changes had taken place in the life history of the salmon of the Shannon which must, of course, have been the result, either directly or indirectly, of the alterations caused by the hydro-electric development.

(*b*) *Nomenclature*

The nomenclature used by workers on salmon in recent years has been adopted throughout this paper. The life of the salmon is normally divided into three periods. First, there is its life in fresh water as a parr, from the time when it is hatched until it assumes the smolt livery and descends to the sea; secondly, there is its life in the sea before it returns to the river to spawn; and thirdly, there is the period which it spends again in fresh water from the time it re-enters the river until it dies after spawning or returns to the seas as a kelt. We know nothing of the details of the second period except what can be determined by scale reading.

Salmon are classified primarily by 'age groups', that is, on the duration of the second period spent feeding in the sea. Those fish which cease to feed in the sea during the winter months and return to fresh water early in the year, or in some cases during the winter months, with reproductive organs only slightly developed, are called 'spring fish', i.e. 'small spring fish', 'large spring fish' or 'very large spring fish', according as they have spent two, three, or four winters feeding in the sea. Those fish which have resumed feeding in the spring of the year in which they re-enter fresh water and which will spawn in the following winter are called 'summer fish'. They are known as 'grilse' or 'peal', 'small summer fish' or 'large summer fish' according as they have spent a little more than one, two or three years respectively feeding in the sea.

The term 'class' is reserved for the various actual age categories of smolts, one-year smolt class, two-years molt class, etc.

2. MATERIAL AND METHODS

It was not found possible to investigate the stocks of salmon for the years 1942 and 1943, but in 1944 a certain amount of material was available from the Shannon. This material was collected in connexion with the determination of the proportion of previously spawned fish in Ireland (Went, 1945*a*) and consisted of a single scale taken from the region of the dorsal fin from each of a large number of salmon, the scales for each month being preserved separately. The scales, preserved in ordinary water, were cleaned with sodium peroxide solution and mounted by means of gelatine solution on microscope slides. As the scales had been taken at random some were useless for age determination, being replacement scales, i.e. scales which have replaced those damaged or lost earlier in life. It was acknowledged that this material was only partially suitable for the purpose of determining the details of the life history of the salmon of the Shannon.

In 1945 full collections of material, comprising sets of scales and data (weight to the nearest 2 oz., length to the nearest $\frac{1}{10}$ in., sex, and date of capture) were made by the management of the Shannon Fisheries (Electricity Supply Board for Éire), the owners of the fisheries of the River Shannon.

It is obviously desirable to follow the variations in the stocks of salmon in this river, but to achieve this end the lengthy investigation of both the age and growth need not necessarily be carried out each year. In 1945 it was therefore decided to determine only the age of the various samples. A single typical scale from each set was selected, cleaned with diluted sodium peroxide solution and mounted on a microscope slide. In this way suitable scales from 769 fish were obtained. The present investigation was based on the combined material from the years 1944 and 1945.

Unlike most investigations on the incoming populations of salmon the actual numbers of fish entering the river are known (see Went, 1943, pp. 152–3), and, therefore, the results may be taken as exactly indicative of the runs of fish and not solely of the fish captured. Examination of the confidential returns of catches during 1944 and 1945 indicates that the samples of material were adequate and fairly representative of the total catches during the fishing season from 1 February to 19 July, and may be used to obtain a good indication of the incoming populations during the year. Operations at Thomond Weir were suspended during part of February 1945, and again at the end of the fishing season, 14–19 July, because of heavy floods; but as the numbers of fish running at both times were small, this has made little difference to the results. The effects of unavoidable fluctuations in the proportion of salmon sampled throughout the season were eliminated by suitable arithmetical adjustments with the aid of the confidential returns. Throughout the tables these weighted figures have been used wherever possible.

Table 1. *Estimated monthly run of fish,* 1941–5 (*as percentages of year's total*)

Month	1941	1942	1943	1944	1945
Jan./Mar.	1·0	4·9	6·3	7·7	8·3
Apr.	5·0	8·1	7·9	8·8	8·1
May	18·2	10·8	5·3	11·2	11·2
June	69·4	70·0	56·6	61·5	55·3
July	6·4	6·2	23·9	10·8	17·1
Total	100·0	100·0	100·0	100·0	100·0

3. RESULTS OF THE ANALYSIS

Runs of fish. As explained in a previous paper (Went, 1943) the returns of Thomond Weir accurately reflect the runs of fish into the freshwater portion of the River Shannon. In Table 1 the estimated monthly runs of fish (as percentages of the total for each year) have been given for 1941–5, and it is obvious that, in general, the form of the distribution was the same in each year. There are some variations in the proportions of the different months from year to year, a matter which will be discussed later.

Table 2. *Percentage of each smolt age in each age group*

	Age group (in winters)					Total maiden fish
Smolt class	1+	2	2+	3	3+	
			1944			
1	6·2	12·2	19·6	23·8	—	8·2
2	77·8	85·4	76·1	76·2	100·0	78·9
3	16·0	2·4	4·3	—	—	12·9
Total	100·0	100·0	100·0	100·0	100·0	100·0
Average age* of smolts in years	2·09	1·90	1·85	1·76	—	1·95
			1945			
1	10·0	12·2	36·6	25·0	—	12·8
2	84·0	81·2	57·3	70·9	—	81·0
3	6·0	6·6	6·1	4·1	—	6·2
Total	100·0	100·0	100·0	100·0	—	100·0
Average age* of smolts in years	1·96	1·94	1·70	1·79	—	1·93

* Based on the assumption that the smolts spent just a complete year, or multiple thereof, before migrating to the sea.

Smolt ages. The distributions of the various smolt classes in the different age groups is shown in Table 2. Three-year smolts in 1944 were more important than the one-year smolts, whereas in 1945 the position was reversed. In both years, however, the two-year smolts formed about 80 % of the total. The proportion of young smolts (one-year olds), in general, increased with a rise in the time spent feeding in the sea. The average age of the smolts in the various age groups decreased as the time spent

feeding in the sea increased. Apart from the small summer fish, there were few differences between the proportions of the various smolt ages in the different age groups in the two years in question, which could not be attributable to normal variations from year to year. Such differences as did occur were well within the fluctuations which might be expected in a normal river. The proportion of 1-year smolts shows no regular change as the season progresses (Table 3).

Smolt types. When dealing with the salmon of the River Shannon for 1927 (Went, 1938) it was mentioned that some of the fish showed marked growth in fresh water in the spring before the smolt migration to the sea took place, whereas others showed little or no such growth. Those fish showing little or no such growth (growth limited to two new growth elements or less) were then described as type A smolts, whereas those fish which showed marked growth in fresh water (more than two new growth elements) were termed type B smolts. In the present material similar observations were made and the division into the two types has been indicated in Table 4. The proportion of type A smolts showed a considerable diminution in 1945, and is the lowest recorded in the investigations on the salmon of this river (Went, 1938, 1940, 1943).

Table 3. *Percentage of 1-year smolts in each month in various age groups in* 1945

Figures in italics indicate results obtained from small number of observations

	Age group (in winters)			
Month	1+	2	2+	Total
Feb./Mar.	—	6·0	—	11·8
Apr.	—	9·6	*60·0*	11·7
May	*8·3*	20·7	36·0	27·9
June	10·4	*0*	*32·0*	10·9
July	9·2	—	*50·0*	10·0
Total	10·0	12·2	36·6	12·8

Table 4. *Estimated proportion (%) of the different smolt types in each smolt class for maiden fish*

	1944		1945	
Smolt age	Type A	Type B	Type A	Type B
One year	—	8·2	—	12·8
Two years	10·2	68·7	5·8	75·2
Three years	9·6	3·3	2·1	4·1
Total	19·8	80·2	7·9	92·1

Table 5. *Estimated monthly catch in each age group as percentage of the yearly total*

	Age group (in winters)						
Month	1+	2	2+	3	3+	With spawning marks	Total
			1944				
Feb./Mar.	—	5·5	—	1·7	—	0·5	7·7
Apr.	—	7·9	0·1	0·4	0·1	0·3	8·8
May	5·4	1·8	3·9	—	—	0·1	11·2
June	59·1	0·4	0·6	—	—	1·4	61·5
July	9·7	—	—	—	—	1·1	10·8
Total	74·2	15·6	4·6	2·1	0·1	3·4	100·0
			1945				
Feb./Mar.	—	6·3	—	1·6	—	0·4	8·3
Apr.	—	7·0	0·4	0·4	—	0·3	8·1
May	0·8	5·7	4·4	0·1	—	0·2	11·2
June	49·5	0·4	1·9	—	—	3·5	55·3
July	15·5	—	0·3	—	—	1·3	17·1
Total	65·8	19·4	7·0	2·1	—	5·7	100·0

Age groups. The incoming populations of 1944 were divided into five groups of maiden or unspawned fish and one group of previously spawned fish, having only one common property, namely, the presence of spawning marks on their scales (Table 5). In the 1945 fish a similar division into age groups was effected, but owing to the absence of the large summer fish (3+winters) there were only four groups of maiden fish. Grilse (1+winters) in each year formed the bulk of the runs of fish with the small spring fish (2 winters) second, followed by the small summer fish (2+winters) (Table 5). These three age groups between them formed more than 90% of the total runs of fish in 1944 and 1945, as they did also in 1941 (Went, 1943). The relatively heavy large spring fish (3 winters) were comparatively unimportant, when conditions now prevailing are compared with those before the year 1929. No comments need be offered as to the proportions of previously spawned fish, which are within the range generally found in Irish rivers (Went, 1945*a*).

In February and March small spring fish formed

about three-quarters of the fish and the large spring fish about one-fifth of the total, the remainder being previously spawned fish (Table 6). By April the small spring fish had increased their proportion in the catch somewhat, and the first members of the small summer fish began to appear. Small summer fish comprised somewhat more than one-third of the bulk of the grilse entered the river in June, small spring fish in April, small summer fish in May and large spring fish in February (Table 7). As would be expected in a river relying mainly on grilse the greatest numbers of previously spawned fish entered the river towards the end of the season, i.e. from June onwards.

Table 6. *Percentage of each age group in the catch of each month*

	Age group (in winters)						
Month	1+	2	2+	3	3+	With spawning marks	Total
			1944				
Feb./Mar.	—	71·4	—	22·1	—	6·5	100·0
Apr.	—	89·9	1·1	4·5	1·1	3·4	100·0
May	48·2	16·1	34·8	—	—	0·9	100·0
June	96·0	0·7	1·0	—	—	2·3	100·0
July	89·8	—	—	—	—	10·2	100·0
Total	74·2	15·6	4·6	2·1	0·1	3·4	100·0
			1945				
Feb./Mar.	—	76·2	—	19·3	—	4·5	100·0
Apr.	—	86·2	4·6	5·5	—	3·7	100·0
May	7·4	50·7	39·5	0·6	—	1·8	100·0
June	89·4	0·7	3·6	—	—	6·3	100·0
July	90·8	—	1·8	—	—	7·4	100·0
Total	65·8	19·4	7·0	2·1	—	5·7	100·0

Table 7. *Percentage of total for each age group in each month*

	Age group (in winters)						
Month	1+	2	2+	3	3+	With spawning marks	Total
			1944				
Feb./Mar.	—	35·2	—	81·0	—	14·7	7·7
Apr.	—	50·6	2·2	19·0	100·0	8·8	8·8
May	7·3	11·6	84·8	—	—	2·9	11·2
June	79·7	2·6	13·0	—	—	41·1	61·5
July	13·0	—	—	—	—	32·5	10·8
Total	100·0	100·0	100·0	100·0	100·0	100·0	100·0
			1945				
Feb./Mar.	—	32·5	—	76·0	—	7·1	8·3
Apr.	—	36·0	5·7	19·2	—	5·3	8·1
May	1·1	29·4	62·8	4·8	—	3·5	11·2
June	75·3	2·1	27·2	—	—	61·3	55·3
July	23·6	—	4·3	—	—	22·8	17·1
Total	100·0	100·0	100·0	100·0	—	100·0	100·0

total catch in May in both years. In 1944, however, the runs of grilse in May were relatively more important than in 1945, and, in fact, than in 1941. From the beginning of June onwards the runs of fish were virtually made up of grilse with a small proportion of other fish, mainly previously spawned fish.

As regards the advent of individual age groups, the It follows, therefore, that in February and March all the fish running were spring fish, in April only a small proportion were summer fish, and thereafter the summer fish predominate (Table 8).

Visual estimations of the proportions of grilse (based mainly on the size) in 1945 made by officers of the Shannon Fisheries at Limerick gave a figure of 71·8%. Having regard to the fact that numbers of

Table 8. *Percentage of spring and summer fish in each month's run of fish*

Month	1944 Spring fish	1944 Summer fish	1945 Spring fish	1945 Summer fish
Jan./Mar.	100·0	—	100·0	—
Apr.	97·8	2·2	95·4	4·6
May	17·0	83·0	53·1	46·9
June	0·7	99·3	0·7	99·3
July	0	100·0	0	100·0
Total	18·5	81·5	22·4	77·6

Table 9. *Absence habit of previously spawned fish*

Absence	Age (in winters) at first spawning 1+	2	3	Total
	1944			
Short (less than a full year)	59	—	—	59
Long (a full year)	—	21	2	23
Very long (more than a full year)	3	—	—	3
	1945			
Short	27	—	—	27
Long	—	4	—	11*
Very long	—	—	—	—

* Including 7 fish of which the age at first spawning could not be determined accurately.

mainly exhibited the short-absence habit (less than a full year), with a few exhibiting the very long-absence habit (more than a full year), whereas the spring fish exhibited the long-absence habit (a full year). These conditions are similar to those prevailing in 1941.

Commercially the small spring fish and higher age groups (i.e. 2, 2+, 3, winters, etc.) are more important than is represented by their proportion by numbers in the catch. The percentage composition by weight in the two years in question is given in Table 10. Apart from the question of weight the earlier running fish (small and large spring fish) fetch much bigger prices per pound than the later running fish, which arrive only when there are comparatively large supplies of fresh salmon on the market.

Divided migration and return. Table 11 gives the years in which the fish were hatched, and it will be seen that in 1944 the 1941 brood contributed over 60% to the total stocks and in 1945 the 1942 brood contributed a like amount. The distributions of the year classes in the two years in question are very similar.

Size distribution. From data available for 1945 the size distribution in each age group was calculated (see Table 12). Those fish having lengths between 21·95 and 25·95 in. formed just over 60% of the total catch and 96% of the total were less than

Table 10. *Percentage composition by weight*

Year	Age group (in winters) 1+	2	2+	3	3+	With spawning marks
1944*	58·5	23·2	7·4	6·3	0·4**	4·2
1945	47·2	28·4	10·7	6·4	—	7·3

* Based on the assumption that the average weights were the same as in 1941.
** Average weight of 25 lb. assumed.

undersized small spring and summer fish may also have been included, this figure agrees quite closely with the value of 65·8% obtained independently.

Previously spawned fish (with spawning marks) are a heterogeneous group, as mentioned earlier, having only one common property, namely, the presence of spawning marks on their scales. All the scales of fish of this group examined (123 for both years) had only one spawning mark. Previous spawners can be best classified on (1) their age at first spawning and (2) the absence habit, or the period spent feeding in the sea between what would have been, but for capture, two successive spawnings.

In Table 9 the previous spawners have been so classified and in general the summer fish (grilse) 33·95 in. in length. As length measurements were not available for 1944 no information as to the size distribution in that year is available. It might be mentioned, however, that the incoming populations in 1945 were, on the average, shorter than those of 1941.

Proportion of the sexes. As mentioned elsewhere (Went, 1938, 1940, 1943) determination of the sex by observation of the external appearance cannot be regarded as really reliable. It affords, at the best, a slight indication of the proportion of the sexes. In Table 13 the proportions of the different sexes, as estimated by this method, have been given for the different age groups.

Average sizes. Monthly details of the average

Table 11. *Divided migration and return (as percentages of the total yearly catch)*

Returned in 1944 as	Hatched in the year 1937	1938	1939	1940	1941	1942	Total
Grilse (1+winters)	—	—	—	11·8	57·8	4·6	74·2
Small spring fish (2 winters)	—	—	0·4	13·3	1·9	—	15·6
Small summer fish (2+winters)	—	—	0·2	3·5	0·9	—	4·6
Large spring fish (3 winters)	—	—	1·6	0·5	—	—	2·1
Large summer fish (3+winters)	—	—	0·1	—	—	—	0·1
Previously spawned fish (with spawning marks)*	0·1	0·6	0·5	2·2	—	—	3·4
Total	0·1	0·6	2·8	31·3	60·6	4·6	100·0

Returned in 1945 as	Hatched in the year 1938	1939	1940	1941	1942	1943	Total
Grilse	—	—	—	4·0	55·2	6·6	65·8
Small spring fish	—	—	1·3	15·7	2·4	—	19·4
Small summer fish	—	—	0·4	4·0	2·6	—	7·0
Large spring fish	—	—	0·1	1·5	0·5	—	2·1
Previously spawned fish*	—	1·6	0·7	3·2	0·2	—	5·7
Total	—	1·6	2·5	28·4	60·9	6·6	100·0

* Approximate values.

Table 12. *Estimated frequency distribution of lengths in different age groups as percentage of the total catch in* 1945

Class interval*	Age group (in winters) 1+	2	2+	3	With spawning marks	Total
20	1·7	—	—	—	—	1·7
22	32·4	—	—	—	0·2	32·6
24	27·0	0·6	0·2	—	1·0	28·8
26	4·7	2·4	0·6	—	1·7	9·4
28	—	7·6	2·1	—	0·6	10·3
30	—	5·7	2·3	—	0·6	8·6
32	—	2·5	1·4	—	0·8	4·7
34	—	0·4	0·4	0·1	0·8	1·7
36	—	0·2	—	1·3	—	1·5
38	—	—	—	0·1	—	0·1
40	—	—	—	0·4	—	0·4
42	—	—	—	0·1	—	0·1
44	—	—	—	0·1	—	0·1
Total	65·8	19·4	7·0	2·1	5·7	100·0

* Class interval 20, etc., includes all fish between 19·95 and 21·95 in., etc.

Table 13. *Percentage of females in the different age groups in the maiden fish*

Age group (in winters) 1+	2	2+	3	Total
62	65	58	33	62

weights and lengths in the various smolt classes and age groups for 1945 will be found in Table 14, to which the following details may be added:

(*a*) Grilse (1+winters). 376 examined:

	lb.	in.	Date captured
Minimum	4·0	21·2	15 June*
Average	5·8	24·0	—
Maximum	9·0	27·7	29 June
	9·5	27·0	18–19 June
	9·5	27·5	

* Several fish of the same weight, with lengths from 21·4 to 22·4 in., were also captured in June.

Table 14. *Mean weights and lengths in the various age groups and smolt classes in* 1945

Month	Smolt age 1 lb.	1 in.	1 *K*	2 lb.	2 in.	2 *K*	3 lb.	3 in.	3 *K*	Total lb.	Total in.	Total *K*
Grilse (1+winters)												
May	7·5	27·5	1·00	5·5	24·1	1·09	6·0	24·4	1·15	5·7	24·4	1·09
June	6·3	24·5	1·17	5·8	23·8	1·15	6·3	24·5	1·18	5·8	23·9	1·16
July	5·6	24·2	1·10	6·0	24·1	1·19	6·1	24·2	1·20	6·0	24·1	1·18
Total	6·2	24·5	1·15	5·8	23·9	1·16	6·2	24·4	1·18	5·8	24·0	1·16
Small spring fish (2 winters)												
Feb./Mar.	11·6	30·5	1·11	10·1	29·4	1·09	12·7	31·3	1·12	10·4	29·7	1·09
Apr.	12·2	30·3	1·15	13·9	30·1	1·13	12·3	30·4	1·21	13·7	30·2	1·14
May	11·4	29·8	1·14	10·7	29·6	1·11	11·3	29·4	1·22	10·9	29·6	1·13
June	—	—	—	10·3	29·3	1·09	—	—	—	10·3	29·3	1·09
Total	11·7	30·1	1·14	11·8	29·7	1·11	12·1	30·4	1·18	11·8	29·8	1·12
Small summer fish (2+winters)												
Apr.	14·4	32·0	1·21	9·8	28·2	1·21	14·0	32·0	1·19	13·7	31·2	1·21
May	12·4	30·9	1·18	12·5	30·6	1·19	11·9	30·0	1·21	12·4	30·7	1·19
June	10·1	29·4	1·09	11·1	29·8	1·09	—	—	—	10·8	29·7	1·09
July	16·0	33·0	1·24	9·0	27·7	1·17	—	—	—	12·5	30·4	1·20
Total	12·5	30·9	1·18	12·1	30·4	1·17	12·3	30·4	1·21	12·3	30·6	1·18

Large spring fish (3 winters)

Feb./Mar. lb.	Feb./Mar. in.	Feb./Mar. *K*	April lb.	April in.	April *K*	May lb.	May in.	May *K*	Total lb.	Total in.	Total *K*
24·9	38·4	1·20	22·5	37·1	1·22	31·0	42·0	1·17	24·5	38·2	1·21

Previously spawned fish (with spawning marks)

	Feb./Mar.	Apr.	May	June	July	Total
lb.	17·3	14·9	14·4	8·0	8·7	10·4
in.	34·9	31·9	32·4	27·2	27·8	29·1
K	1·12	1·22	1·15	1·09	1·08	1·11

(*b*) Small spring fish (2 winters). 240 examined:

	lb.	in.	Date captured
Minimum	5·0	23·9	22 May
Average	11·8	29·8	—
Maximum	22·0	37·2	20 April
	22·75	35·3	8 May

(*c*) Small summer fish (2+winters). 80 examined:

	lb.	in.	Date captured
Minimum	6·0	24·6	5 June
Average	12·3	30·6	—
Maximum	22·0	35·5	15 May

(*d*) Large spring fish (3 winters). 24 examined:

	lb.	in.	Date captured
Minimum	20·0	35·3	24 April
	20·0	36·5	26 April
Average	24·5	38·2	—
Maximum	31·0*	42·0	30 May

* The largest fish recorded for 1945.

(*e*) Previously spawned fish (with spawning marks). 37 examined:

	lb.	in.	Date captured
Minimum	5·0	23·5	8 June
Average	10·4	29·1	—
Maximum	20·0	35·4	3 March

Condition coefficients. The method of determining the condition coefficient or the relationship between weight and length was described in previous publications (Went, 1938, 1940, 1943). In Table 15 the mean monthly condition coefficients in the various age groups have been given, the details having been extracted and calculated from previous tables.

The average condition coefficients were approximately the same in the spring and summer fish, the actual calculated differences being insignificant and only discernible in the third decimal place. As was found previously the large spring fish had the highest condition coefficient (1·21), but the average condition

Table 15. *Mean condition coefficients in the different groups in* 1945

	Age group (in winters)					
Month	1+	2	2+	3	With spawning marks	Total
Feb./Mar.	—	1·09	—	1·20	1·12	1·12
Apr.	—	1·14	1·21	1·22	1·22	1·15
May	1·09	1·13	1·19	1·17	1·15	1·15
June	1·16	1·09	1·09	—	1·09	1·15
July	1·18	—	1·20	—	1·08	1·17
Total	1·16	1·12	1·18	1·21	1·11	1·15
Spring fish			1·15			
Summer fish			1·15			

coefficient of the age groups as a whole was about 5% lower than in the years previously investigated (Went, 1938, 1940 and 1943).

Erosion. Erosion, or more properly absorption of the material of the scales of a salmon, takes place during a sojourn in fresh water, although it may also take place in the sea if the fish is prevented from entering the river for any reason. In the 1945 material only four fish showed slight erosion of the scales: up to 3° on Menzies' Scale in two small spring fish and a large spring fish on 28–30 May and in a small summer fish on 2 July.

4. GENERAL DISCUSSION OF THE RESULTS AND THEIR APPLICATION

It might be suggested that Table 1 indicates some slight progressive change in the incoming populations in the years in question, in that the proportion of fish entering the river in the early months (January–April) shows an increase from 1941 to 1945. In Table 1 we are dealing with the *proportion* of the fish which run each month compared with the total runs. However, the returns of catches from Thomond Weir show that there was no increase in the actual *numbers* of spring fish. Normally the bulk of the fish running before 21 May are spring fish and thereafter the runs consist of summer fish (grilse, small summer fish with a small proportion of previously spawned summer fish). The relative numbers of fish running up to and including 20 May each year are given below, the runs from 1 January to

Period	1941	1942	1943	1944	1945
1 Jan. to 20 May inclusive	100	136	133	108	70
21 May to 19 July inclusive	857	662	670	408	228
Whole year	957	798	803	516	298

20 May 1941 being regarded as 100. These figures differ from those given by Went (1945*b*) since they have been corrected for those short periods when Thomond Weir was out of commission because of floods. Although there was an increase from 1941 to 1942 in the numbers of spring salmon running, a decrease set in from 1943. The fluctuations in the numbers of spring fish are well within the range expected in a normal river.

A comparison between the present results and those obtained for 1941 (Went, 1943) yields no evidence that the incoming populations of salmon of the River Shannon were in course of undergoing very marked changes. The differences observed in the stocks of fish in the years 1941, 1944 and 1945 are such as one finds in stocks of salmon in normal rivers, which have not been changed by man's activities. It is regrettable that material for 1942 and 1943 was not available; but Fig. 1 shows that conditions generally did not differ markedly from those prevailing in 1941, 1944 and 1945. The distribution of fish over each season from 1941 to 1945 has been given, each month being divided up into three periods: days 1–10, 11–20 and 21 to the end of the month. The peak of the runs of fish into the Shannon is now invariably in June, usually in the second or third periods. The general form of the five curves given in Fig. 1 is the same although there are marked fluctuations, from year to year, in the actual number of fish entering during any one period of a month. It might be mentioned that in 1943 the grilse runs in Ireland were considerably later than usual, and the Shannon in this respect showed the same phenomenon. The exceedingly poor runs in 1945 into the Shannon had a parallel over the whole country, as the runs (and catches) were the poorest for many years.

We have now established that the 1941 results may be regarded as an accurate picture of the present stocks of salmon in the River Shannon. This leads us to consider a further problem of the salmon of this river which may be stated briefly as follows. As a consequence of the alterations made in the Shannon

to develop its hydro-electric resources the salmon of the river exhibited certain changes. First there was a marked decrease in the number of fish running the river and secondly most of the fish now run in

Fig. 1. Curves showing the runs of fish into the River Shannon in 10-day periods (A = days 1–10; B = days 11–20; and C = days 21 to last day of month). All curves are plotted to same scale from confidential data.

whether there has been an actual loss or reduction of some groups of fish, leaving other groups unaltered, or alternatively whether there has been a definite change from spring running to summer running, June, whereas in former days, although June may have had bigger runs than any other month, the earlier months were also very important (Went, 1943, Fig. 4, p. 165). The question to be solved is thus augmenting the runs of summer fish. Unfortunately, we have no information available as to the actual strength of the runs of salmon into the Shannon before 1929, nor could such information

have been obtained since there was no suitable counting weir on the river until Thomond Weir was completed in 1940. Resort must be had, therefore, to the confidential returns under the Statistics Act, 1926, and subsequent Orders made thereunder.

Ireland is divided up into a number of Fishery Districts, each in charge of a Board of Conservators. The Limerick or No. 8 District which covers the tideway and catchment area of all the rivers flowing into the sea between Dunmore Head, Co. Kerry and Hag's Head, Co. Clare, contains the Rivers Shannon, Cashen, Maigue, Deel, Fergus, Bunratty and a number of rivers of lesser importance. Fishing by means of commercial engines, drift nets, stake nets, draft nets and Thomond Weir occurs in the estuary and tideway of the Shannon and tidal portions of the Rivers Maigue, Deel, Fergus and Bunratty which empty into the Shannon Estuary. The Limerick District consists of three distinct sections which, for the purpose of this discussion, may be conveniently grouped as (1) the Cashen and its tributaries, (2) the Limerick Fishery District less the River Cashen and its tributaries. This group consists of the Shannon, its estuary and the rivers flowing into this estuary, and a number of small rivers both north and south of the Shannon Estuary which are relatively unimportant (see Fig. 2).

For alternate years from 1927 the statistics of salmon, sea trout and eels have been published by the Department of Agriculture (Éire, 1944). The salmon returns for the Limerick District have been examined in detail and the results are given in Table 16 and Fig. 3. It will be seen that there was a fall from 1931 until 1939, followed by a lesser rise in 1941. The low level reached in 1937 and 1939 was due, partly, to the fact that fishing in the Shannon proper was curtailed in an attempt to provide adequate breeding stocks for the river. The catch in the Cashen and its tributaries, which was unaffected by the Shannon hydro-electric scheme, contributed from 17% (in 1927) to 67% (in 1939) of the total weight of salmon caught in the Limerick District. There is no indication of a marked variation in the captures in the Cashen which used to account for about 20–25% of the total weights of fish captured in the Limerick District. In the Shannon, Maigue, Deel, Fergus, Bunratty and a number of rivers of lesser importance combined, the catch fell from 414,000 lb. (in 1927) to 42,000 lb. (in 1939), the main cause of the decrease being the decrease in the runs of salmon to the main Shannon, which was brought about by the erection of the Shannon hydro-electric plant.

Our earlier information on the salmon of the River Shannon is mainly derived from the years 1927 and 1928 (Went, 1938, 1940), but from the point of view of this discussion the 1928 results are presented in a more suitable form. If we assume either that the 1928 catch in the Limerick District was the mean of that for 1927 and 1929, or was the same as that for 1931 (about 400,000 lb. in each case), then with the catch of the Cashen and its tributaries at about 90,000 lb. (the average for 1927–43), the remainder of the Limerick District would account for 310,000 lb. In 1941 the catch for the Limerick District was 266,500 lb., the Cashen and its tributaries contributing almost exactly 50% of this amount. The catch in the rest of the Limerick District was therefore 133,300 lb., a reduction of 57% on that of 1928. If we can judge from the export figures for Éire, the catches in 1941, for the country as a whole, were slightly better than those for 1928; but ignoring this difference it is obvious that there has been a considerable decrease in the total catch in the Shannon proper. Information is also available for 1927, 1929 and 1931, when the runs of fish were not affected by the operation of the Shannon hydro-electric scheme and for 1942. Using this information we can obtain an approximate idea of the numerical distribution of fish over the season in the Shannon, in the years both

Table 16. *Returns from the Limerick District*

Year	Catch in lb. in Limerick District	Catch in lb. in Cashen and tributaries	Catch in lb. in Limerick District less Cashen and tributaries	Proportion of catch contributed by Cashen and tributaries %
1927	499,300	84,700	414,600	17
1929	307,500	68,000	238,900	23
1931	415,100	128,700	286,400	31
1933	295,600	71,000	224,600	24
1935	272,700	120,000	152,700	44
1937	125,100	73,000	51,300	59
1939	127,500	85,000	42,000	67
1941	266,500	132,200	133,000	50
1943	264,700	121,800	142,900	46

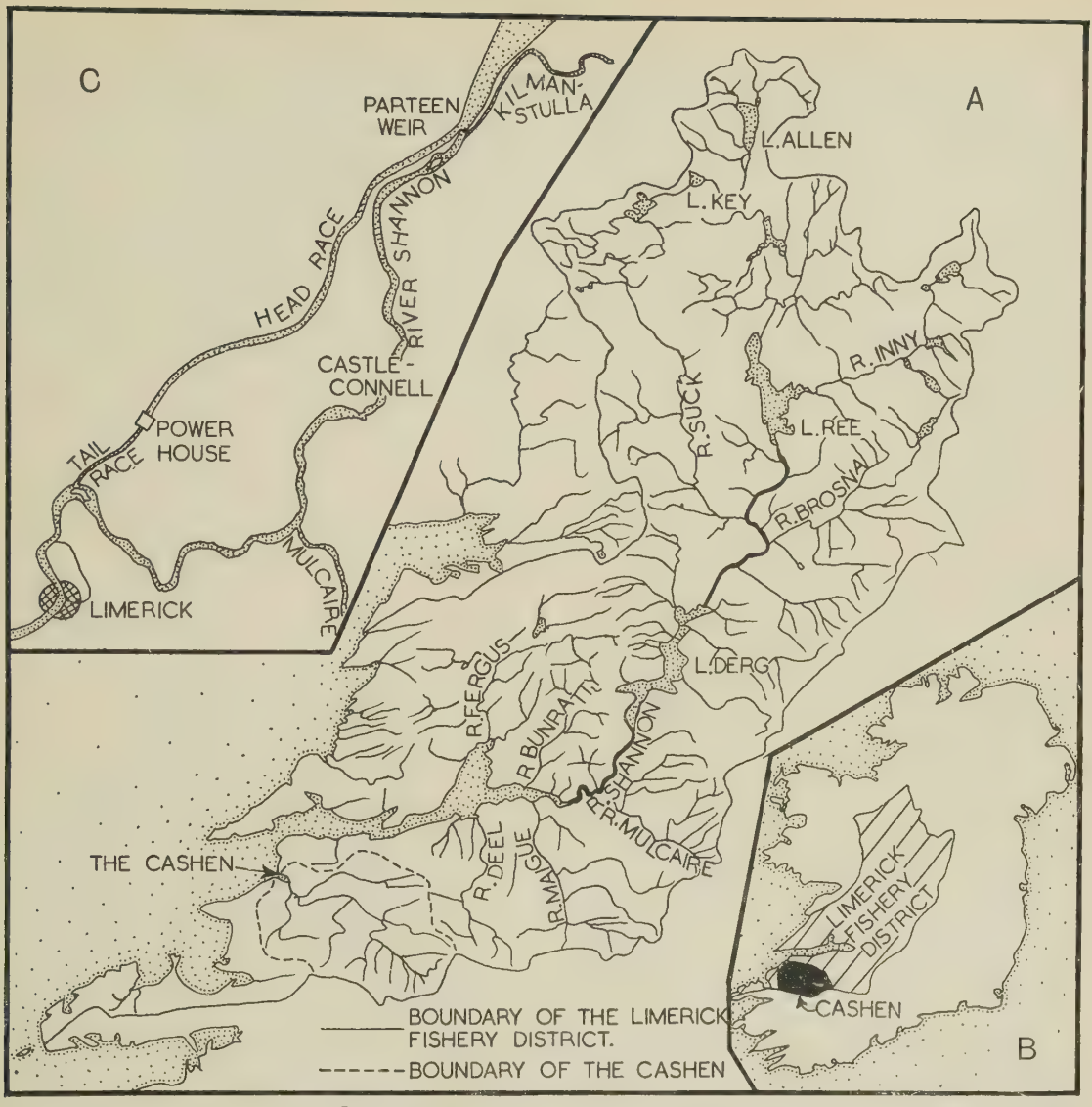

Fig. 2. A. The Limerick Fishery District showing the more important rivers and tributaries of the River Shannon. Scale approx. 27·5 miles per in. B. Sketch map of Ireland showing Limerick Fishery District and the Cashen. C. Sketch map showing layout of waterways connected with the Shannon hydro-electric plant. Scale approx. 2·75 miles per in.

Table 17. *Comparative catches in the Shannon for the years* 1927–9, 1931* *and* 1941–5
(1928 *total taken as* 100)

	Year	Jan./Mar.	Apr.	May	June	July	Total
Pre-Shannon scheme	1927	25·3	33·2	35·3	36·6	3·6	134·0
	1928	18·9	24·8	26·3	27·3	2·7	100·0
	1929	13·9	18·4	19·5	20·2	2·0	74·0
	1931	17·4	22·8	24·2	25·1	2·5	92·0
Post-Shannon scheme	1941	0·4	2·2	7·8	29·8	2·8	43·0
	1942	1·8	2·9	3·9	25·2	2·2	36·0
	1943	2·3	2·9	1·9	20·4	8·6	36·1
	1944	1·8	2·0	2·6	14·3	2·5	23·2
	1945	1·1	1·1	1·5	7·4	2·3	13·4
Average	1941–4	1·6	2·5	4·0	22·4	4·0	34·6

* The figures for 1927–9 and 1931 calculated on basis that distribution over the season was the same as for 1928.

before and after the operation of the hydro-electric scheme (Table 17 and Fig. 4). (The returns for 1945 were purposely left out of Fig. 4 as the yield of salmon in that year in most rivers in Ireland was probably the lowest within living memory.)

It is clear that there has been a loss in the earlier running fish and not a transformation from early running to late running as has often been suggested. An idea of the relative numbers of the different age groups of salmon running into the Shannon can be calculated, using the data given in the last column of Table 17 and the other data made available in our investigations into the biology of the Shannon salmon (Table 18, and Fig. 5, again omitting 1945). Obviously there has been a reduction in the numbers of heavy salmon consequent on the erection and operation of the hydro-electric plant, only the grilse showing little alteration. This is an important conclusion because it furnishes a starting point for future development of the river. What alterations have there been in the river as a result of the erection (and operation) of the hydro-electric plant? These alterations may be considered under five heads.

started to work smolts from the upper waters found difficulty in passing down the river. Special fry guards were erected for use at Parteen Weir, at the top of the headrace, but the smolts refused to avail themselves of the facilities provided by the fish pass (Fig. 2C). In consequence large numbers of smolts from the upper waters were destroyed for many years. This matter has now been rectified and the smolts are allowed into the headrace from which they are enticed at night into the ship's lock, adjacent to the Power House at Ardnacrusha, by powerful arc lights.

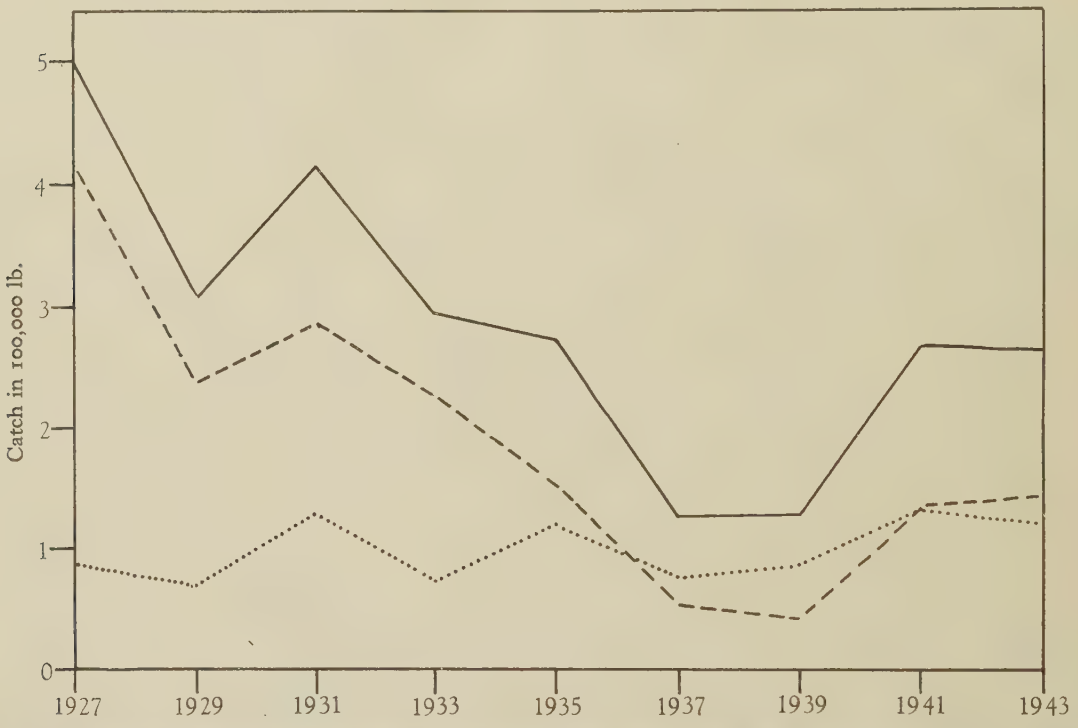

Fig. 3. Curves showing weight of salmon captured in alternative years from 1927 to 1943 in the Limerick Fishery District and various parts thereof. Full line = catch in Limerick Fishery District. Dotted line = catch in the Cashen and its tributaries. Broken line = catch in the Limerick Fishery District less the Cashen, etc.

(1) *Obstruction of the descending smolts.* For a number of years after the hydro-electric plant

(2) *Obstruction and diversion of the ascending fish.* Salmon entering the River Shannon have shown a marked preference for the tailrace channel under most water conditions, and large numbers run up to the Power House at Ardnacrusha, Co. Clare. Although some of these fish do drop back and enter the main river, many do not, and hence their potential progeny are lost. Attempts were made at one time to operate an electrical barrage at the downstream end of the tailrace, but owing to the peculiar conditions this was not successful. The number of fish involved is a matter for conjecture, as no actual method of computing this loss has been

Table 18. *Estimation of the relative numbers of fish in the different age groups running into the Shannon in certain years. (The 1928 total taken as 100)*

		Age groups (in winters)							
	Year	1+	2	2+	3	3+	4	With spawning marks	Total
Pre-Shannon scheme	1927*	33·1	41·7	20·2	26·7	0·1	0·9	11·3	134·0
	1928	24·7	31·0	15·2	19·9	0·1	0·7	8·4	100·0
	1929*	18·3	22·9	11·3	14·7	0·1	0·5	6·2	74·0
	1931*	22·8	28·5	14·0	18·3	0·1	0·6	7·7	92·0
Post-Shannon scheme	1941	32·2	3·9	4·1	0·3	—	0·1	2·4	43·0
	1942†	27·0	3·2	3·4	0·3	—	0·1	2·0	36·0
	1943†	27·1	3·2	3·4	0·3	—	0·1	2·0	36·1
	1944	17·2	3·6	1·1	0·5	‡	—	0·8	23·2
	1945	8·8	2·6	0·9	0·3	‡	—	0·8	13·2
Average	1941–4	25·8	3·5	3·0	0·4	—	0·1	1·8	34·6

* Same distribution of age groups assumed as in 1928 (Went, 1940).
† Same distribution of age groups assumed as in 1941 (Went, 1943).
‡ Less than 0·05.

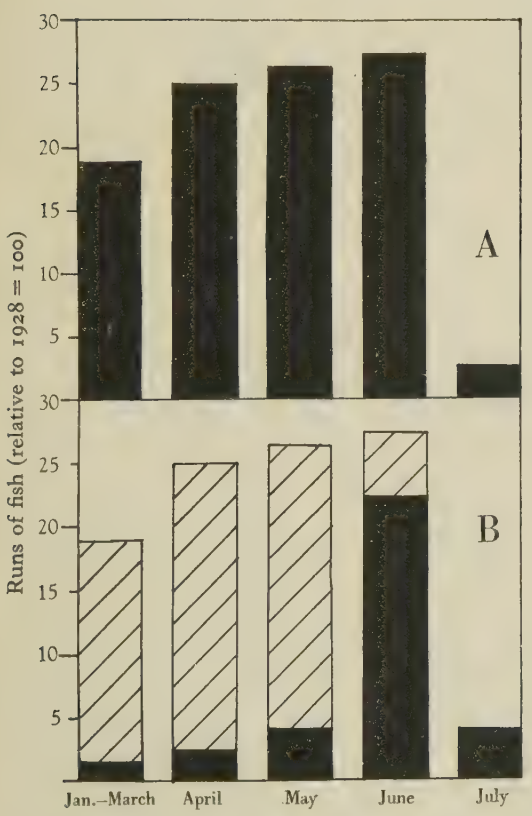

Fig. 4. Diagrammatic representation of the monthly catches of salmon (A) before and (B) after the advent of the Shannon scheme. (Black areas = catches (in relative units—see Table 17). Cross-hatched areas = missing portion of catches.)

evolved, but it obviously was and probably still is, a serious loss to the fishery.

(3) *Changes in the discharge of water.* Since the operation of the hydro-electric scheme, heavy floods in the old channel of the River Shannon between Parteen Weir and the end of the tailrace have been virtually unknown, owing to the impounding of water in the Shannon and Lough Derg. There is, therefore, a tendency to the maintenance of a steady flow, in addition to the discharge from the Kilmanstulla River, which now empties into the Shannon below Parteen Weir.

(4) *Destruction of the spawning facilities.* Prior to 1929 the spawning beds below Parteen Weir were the most important in the whole river. The channel at this time was wide, particularly in the Castleconnel area, with a large flow of water during the spawning season. Immediately the hydro-electric scheme was put into operation the discharge down the old channel was reduced considerably, with the consequence that considerable portions of the original bed of the river became dry for part, or the whole, of the spawning season. In consequence, in the early stages of the 'Shannon scheme' a considerable portion of the ova deposited in this region was left high and dry and did not mature.

(5) *Changes in the feeding conditions.* No detailed information is available on this subject. It is difficult to believe that any important change could have occurred in this respect above Parteen Weir, except inasmuch as the shallow stretches of the river immediately above the intake works are now flooded to the extent of several feet. In the old channel, between the head- and tailraces, feeding conditions have been adversely affected by the reduced area of water.

The obstruction and destruction of the smolts from the north of Ardnacrusha, Co. Clare, in the early stage of the 'Shannon scheme' obviously meant a reduction in the future stocks of the river. These losses due to the initial destruction of smolts in 1930 and subsequent years would have first been felt to a very slight extent in 1931, to a more marked extent in 1932, and would reach a maximum some time later. Similarly, the failure of fish in the tailrace to spawn and the loss of ova on the Castleconnell spawning beds would react adversely on the future stocks. The effect of this would not have become apparent until 1934 and would have become more important in 1935 and 1936.

In the light of the foregoing information the reduction in the stocks of salmon in the River Shannon as a result of the hydro-electric scheme is not difficult to accept. We must now consider the differential loss of the heavy salmon, i.e. salmon which have spent two or more years feeding in the sea.

Prior to the erection of the hydro-electric plant salmon ascended the River Shannon and spawned in quantity in some of the upper parts of the river. Even at Lough Key in the upper reaches there was a profitable net fishery in the lake, and large numbers of salmon spawned in the Boyle River and in certain rivers flowing into Lough Allen. To-day only a limited number of salmon ascends the Parteen Weir fish pass, though it is well designed (Hassard, 1937). In former days hundreds of large fish spawned in the Castleconnell area, whereas to-day spawning is obviously considerably limited. The main spawning region in the River Shannon is the tributary, the Mulcaire, a river which to-day, as formerly, is known mainly as a resort of grilse. It is difficult to believe that the loss of the spawning facilities for large salmon at Castleconnell and the transfer of the main spawning activities to a tributary of the Shannon which was always known as the haunt of grilse was a mere coincidence. The writer feels that in these changes are to be found the basis of the alterations in the character of the runs of salmon into the Shannon since the inception of the hydro-electric plant.

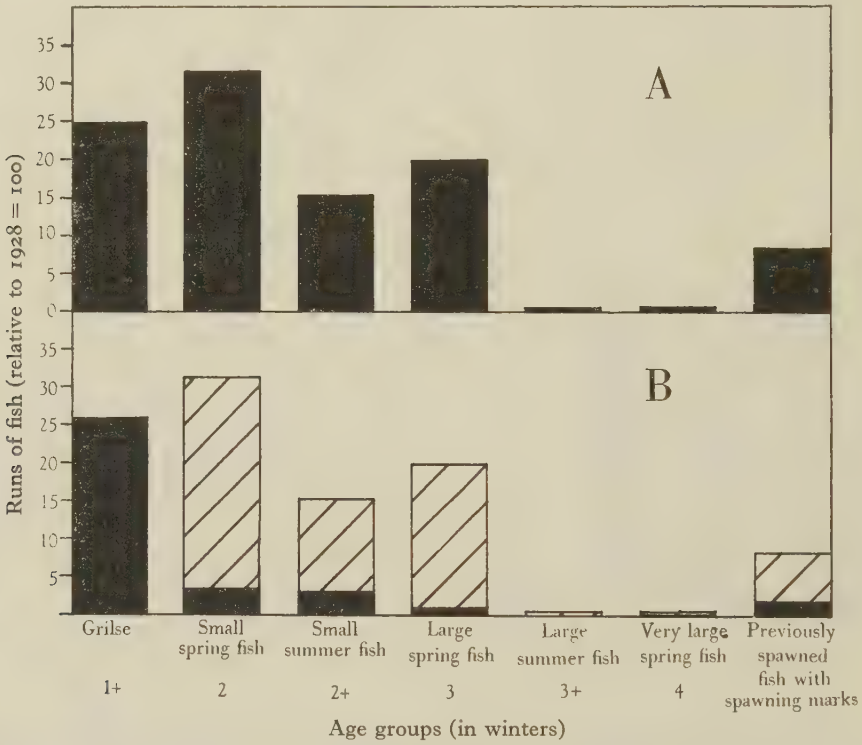

Fig. 5. Diagrammatic representation of the catches in the different age groups (A) before and (B) after the advent of the 'Shannon scheme'. (Black areas = catches (in relative units—see Table 18). Cross-hatched areas = missing portion of catches.)

The investigations on the River Shannon add nothing to our knowledge of whether 'spring fish breed spring fish'; but experience on the Shannon indicates two possibilities: (1) That spring fish

breed spring fish and that their heavy destruction in the Castleconnell area in the early years has reduced their subsequent numbers. (2) That the particular environmental conditions prevailing during the early life of a salmon determines the time of its return to fresh water, and that conditions in the Shannon are now such as would produce grilse or late-running fish.

5. SUMMARY

1. The age distribution of salmon captured in the River Shannon in 1944 and 1945 and the mean sizes and condition coefficients of the various age groups in 1945 were calculated. The bulk of the fish belong to the two-year smolt class, but the one-year smolts were quite important, forming 8·2 and 12·8% in the two years in question. In 1944 the proportion of three-year smolts was abnormally high. Grilse (fish which have spent just over a full year feeding in the sea) were the most important age group, forming two-thirds or more of the total catch. The next most important age group was the small spring fish (two complete years feeding in the sea).

2. Information on the catches of salmon in the River Shannon during 1927–45 shows that since the inception of the hydro-electric scheme there has been a considerable reduction in the numbers of fish which have spent two or more years feeding in the sea.

3. The loss of these heavy fish has materially decreased the total catch, which in 1941, for example, was about 60% less than in 1928.

4. The grilse appear to have remained more or less constant since 1927.

5. It has been suggested that the changes in the character of the runs of salmon into the River Shannon since the construction and operation of the hydro-electric plant were due to the destruction of the important spawning facilities for large salmon at Castleconnell and the transfer of spawning activities to a tributary of the Shannon which was noted for being the haunt of grilse prior to the erection of the hydro-electric plant.

6. ACKNOWLEDGEMENTS

I am indebted to Mr Liam Forde, Shannon Fisheries, Limerick (Fisheries Director of the Electricity Supply Board of Éire), for collecting the material on which this investigation was based and for his kindness in undertaking to continue collection of material in future years for annual checks of the age and growth of the salmon of the River Shannon.

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THE HABITATS AND TOLERANCE RANGES OF *LYMNAEA* (*RADIX*) *CAILLAUDI*, THE INTERMEDIATE SNAIL HOST OF LIVER FLUKE IN EAST AFRICA

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(With Plates 5–8 and 4 Figures in the Text)

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1. INTRODUCTION

Lymnaea (*Radix*) *caillaudi* Bgt. is the East and Central African relative of *L. natalensis* Krs. This latter species occurs typically in South Africa, where it has been shown by Porter (1920*a*, *b*, *c*) to be the most important intermediate snail host of *Fasciola gigantica*, the common liver fluke of sheep and cattle both in South, Central and East Africa.

Both *caillaudi* and *natalensis* belong to the subgenus *Radix* Montf., and the name *caillaudi* is that given to this northern form by Conolly (1939); I employ it in this paper because most Kenya specimens of *Lymnaea* appear to be referable either to this form or the '*elmeteitensis*' Smith type of shell, although a long series of measurements of specimens from different localities in Kenya appears to indicate that the status of *caillaudi* as a distinct species should be revised, both *caillaudi* and *elmeteitensis* being hardly more than racially distinct, or on a south-north cline, from true *natalensis*.

Whatever its true systematic position may be, there can be little doubt that *Lymnaea caillaudi* is a most efficient intermediate host for liver fluke in Kenya Colony. Collections of this snail from various localities in Kenya where fluke is prevalent have yielded infection rates with the larval stages of *Fasciola* up to 60% positive; infection rates of about 40% are not uncommon, while the average for all fluky localities so far examined is between 15 and 20%. Experimental infections of guinea-pigs in this laboratory with cercariae released from such naturally infected *Lymnaea* have shown the identity of such cercariae, adult *Fasciola gigantica* having been

obtained post-mortem from the experimentally infected animals.

Data on the prevalence of liver fluke in East Africa are difficult to obtain owing to the uncertainty of the exact place of origin of most abattoir-slaughtered native cattle, and the fact that fascioliasis is seldom recorded as such, most livers being recorded as 'condemned' only with no reason stated. Such abattoir records as have been carefully certified, however, indicate that the disease is common in most parts of the Kenya Highlands, the northern and eastern parts of Uganda and the highlands of Tanganyika. While most European stockowners recognize the disease and know its cause, and the fact that it is transmitted by snails, considerable misunderstanding appears to exist as to where such snails may be found and the type of locality in which fluke may be expected. The epidemiology of the disease is clearly bound up with the type of habitats favoured by the snail which transmits it, and beyond a statement, which is misleading for Kenya conditions, that the snail 'favours stagnant water' (Vety. Dept. 1944), no account exists of the habitats of the vector species in Kenya Colony. It has been the purpose of this study to determine in which localities this snail may be found and to define its habitat preferences more precisely; armed with this knowledge, control of the snail, and thus the disease it carries, can be more efficiently undertaken.

2. GEOGRAPHICAL DISTRIBUTION OF *LYMNAEA CAILLAUDI*

Conolly (1939) records *caillaudi* from a few localities in South Africa, Blackie (1932) has recorded it from near Salisbury, Southern Rhodesia, while Mozley (1939, 1944) has given its distribution in general terms as covering Egypt, Abyssinia, Tanganyika, Zanzibar and Southern Rhodesia (specimens from this last area being recorded by this author as 'near *natalensis*'). Gordon, Davey & Peaston (1934) record *L. elmeteitensis* (see remarks above about the status of this 'species') from Kabala and Berekoro in Sierra Leone. Pilsbry & Bequaert (1927) indicate a very wide distribution in the 'Ethiopian region', where it avoids the rain-forest belt, and record it more specifically from the Belgian Congo (*L. natalensis undussumae*, again a 'species' which appears barely separable from *caillaudi* as noted by these authors themselves). *L. caillaudi* is common in Kenya Colony, and specimens which I noted in Madagascar appear also to belong to the same species group. It almost certainly occurs in Uganda and Somalia, probably north to British Somaliland and Eritrea, and south to Portuguese East Africa where it will merge with true *natalensis* and the South African *caillaudi* localities. It is clearly a species which extends over immense areas of Africa, regardless of watersheds (Pilsbry & Bequaert, 1927); within Kenya Colony I have specimens from all the main watersheds east and west of the Rift Valley in the Highlands, Lake region and Northern Frontier District, but as yet from only a few localities in the Rift Valley itself. I have no information about its occurrence in the Coast Province, but there is no reason why it should not occur there, having been recorded from coastal areas in Tanganyika and Zanzibar (Mozley, 1939). It is scanty in the Northern Frontier District owing to the absence of suitable habitats in this desert country, though it is abundant in certain valleys on Marsabit Mountain in the Northern Frontier District. It will probably be found wherever suitable habitats are available in Kenya Colony.

It is of interest that the Palaearctic fluke vector snail (*L.* (*Galba*) *truncatula* (Müller)) also occurs in Africa, being recorded from South Africa (Conolly, 1939; Gilchrist, 1918) and Lower Egypt (Pilsbry & Bequaert, 1927), and I have specimens from a locality near Lake Solai in the northern portion of the Rift Valley in Kenya and from the Veterinary Laboratory grounds at Kabete in Kenya, which appear to be referable to this species. It is obviously an introduction from Europe, and while it may have been overlooked in other parts of Africa owing to its small size, it is probably too rare as yet to be of any economic importance in this country. Porter (1925) has shown that *L. truncatula* may also act as a vector in South Africa.

Pl. 5 shows a typical series of *L. caillaudi* shells from Kenya Colony; this is a readily recognizable snail, since no other dextral shell (i.e. with the aperture to the right when the spire is held upwards with the aperture facing the observer) resembles it in this Colony, except species of *Succinea*; these latter, however, are very uncommon, are not truly aquatic, have a more elongate wider aperture than *Lymnaea* with a relatively short spire, and in life have a whitish coloured foot compared with the slaty-grey foot of *Lymnaea* and short black-tipped club-like tentacles on the head compared with the flat triangular grey tentacles of *Lymnaea*.

Species of *Fasciola* causing liver-rot are practically cosmopolitan in distribution, and in the various parts of the world where fascioliasis occurs, the snail hosts are almost always a member of the family Lymnaeidae. The habitats and biology of these diverse vector species of Lymnaeidae vary widely in different parts of the world and have been usefully summarized by Olsen (1944). Of all these snail hosts capable of transmitting liver fluke, *Lymnaea caillaudi* most closely resembles the Palaearctic vector *L. truncatula* in bionomics, though its various 'forms' in the Ethiopian region differ amongst

themselves in habitat preference (p. 177). Fortunately for comparative purposes, the biology and ecology of *L. truncatula* have been more intensively studied than those of the vector species in other countries, notably by Walton (1918), Atkins (1923), Atkins & Lebour (1923), Walton & Jones (1926), Walton & Wright (1926), Lührs (1933*a*, *b*), Mehl (?1932, 1933), Schmid (1934), Økland (1936), Wertheim (1937, 1938, 1941), Wertheim & Rukavina (1938), Peters (1938) and Hatzky (1940). Boycott (1936) gives the most comprehensive review of the habitats of fresh-water Mollusca with particular reference to British conditions; these, however, apply also in general to tropical and subtropical conditions.

Fresh-water ecological studies on aquatic molluscs in the Ethiopian region have been very scanty, the best general review being that of Pilsbry & Bequaert (1927) with special reference to Congo conditions. Cunnington (1920) has dealt with the lake Mollusca, more particularly those of Lake Tanganyika, and Mozley (1939, 1944) has dealt in general with other fresh-water Mollusca in Tanganyika, Zanzibar and Southern Rhodesia. Most specific ecological studies of fresh water in Africa have been directed to the vector snails of human schistosomiasis, such as those of Leiper (1918), Cawston (1920, 1924, 1925, and numerous other notes since that date), Porter (1920*b*, 1938), Blackie (1932), Gordon *et al.* (1934), Haslam (1929) and Barlow (1937).

Cawston (1920, etc.) and Porter (1920*b*, 1938) give a few notes on the habitats of *L. natalensis* in South Africa; but critical studies of environmental factors influencing the distribution of *Lymnaea* in Africa are lacking.

3. THE HABITATS OF *LYMNAEA CAILLAUDI* IN KENYA COLONY

(*a*) *Habitats available*

The map in Fig. 1 is a generalized composite diagram of the range of aquatic habitats available in valleys in Kenya Colony, either in the coastal, highland or lake province areas, and the characters of each type in this range will be dealt with in turn. It should be relatively easy to assign a particular habitat, on say a farm, to its position in this scheme, though of course variations in 'proportion' may occur, e.g. the tributary stream may enter a swamp instead of a main river and so on, but this does not alter the features of any one particular part.

A. In a typical valley, the headwaters of a tributary stream have almost invariably a seepage origin on a hillside, a 'marshy' type of seepage in short grass, or occasionally *Cyperus* or *Juncus* sp. reeds, with—if the seepage is an open one—clear water trickling in shallow runnels and from small pools interconnecting and much divided. If the seepage head is 'closed' with dense reeds, the water is stagnant, shallow and turbid with a heavy red scum of Ferrobacteria and occasionally impregnated with marsh gases. The latter type is uncommon, and has an outlet portion corresponding to an open seepage.

B. This seepage head then develops into a narrow-channelled torrential portion with steep eroded clay or rock banks, obviously subject to scouring floods and rapid alteration of water-level, usually with a swift current and a clean-swept bottom of fine gravel or stones.

C. About the lower level of this torrential portion and anywhere below it, several other seepages may occur along the river banks, essentially similar in features to habitat A, and up to an acre or more in extent (Pl. 6, photo 1; Pl. 7, photos 1, 2).

D. Very often, particularly in native reserves, habitats A and C are cleared and channelled to make small or large irrigated *shambas* in which vegetables, bananas or sugar cane are grown. The channels are well defined, shallow with slow-flowing water, and usually with a certain amount of aquatic vegetation except in those *shambas*, where the channels are cleared of vegetation two or three times a year. They may or may not have a heavy growth of iron bacteria, usually subaquatic if present owing to the slight current preventing scum formation. Such channels have a mud bottom (Pl. 8, photo 4).

E. The torrential portion then flattens out on a level portion of the valley to become a meandering, much divided, shallow stream with a slight current, and low sparse reeds or grass and open water on a muddy bottom, the water being clear. Such places are favourite watering places for stock (Pl. 6, photos 3, 4; Pl. 7, photo 3).

F. The tributary valley is often joined by another tributary valley about this level which may be of a different type, often large but with no permanent streams running through it, the water being in a series of disconnected pools, stagnant, turbid and with a heavy growth of iron bacteria. The stream is intermittent, flowing only in wet weather, the pools which are left in the dry season often being dammed back and used for watering stock—in which case they are foul and turbid with no vegetation or iron bacteria present and are much puddled by cattle.

G. Occasionally a small 'relict' pool is left by a high-water flood out of the main stream channel, the bottom being rocky or muddy (Pl. 8, photo 1).

H. Hillside seepages are occasionally opened up along the valley sides to form small washing pools which may have clear spring water if used for drinking, or turbid and soapy water if used for washing (Pl. 6, photo 2).

I. The trickle from such washing pools forms a short meandering shallow stream resembling a true seepage, with a muddy bottom.

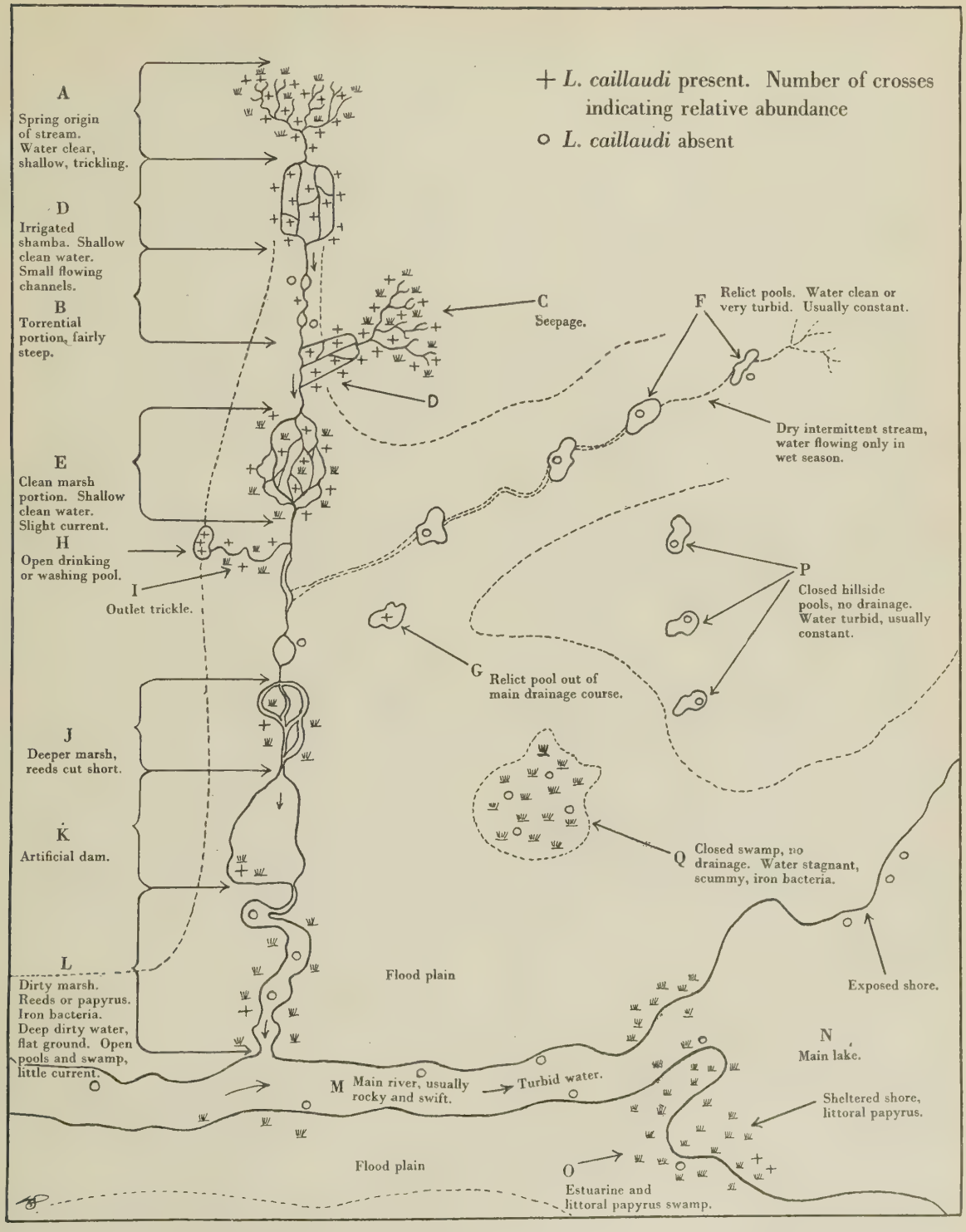


Fig. 1. Diagrammatic representation (not to scale) of main dry-season habitats of *Lymnaea caillaudi* in Kenya Colony.

J. As the main tributary flows on, it becomes deeper and more slow with denser reed beds, but these reed beds may be cut back short as in some tsetse-cleared areas or to provide thatching, and this part of the stream may then resemble habitat E, except for depth.

K. The main tributary may be dammed up to provide water for a flour mill or for other uses, the dam being open water up to an acre or more in extent with occasional patches of reeds.

L. The stream generally becomes wider, deeper and more mature with dense papyrus or reed beds and stagnant marshy edges, the open water having very little current, being stagnant and scummy with iron bacteria, much vegetable detritus and sub-aquatic vegetation such as lace plants. The bottom is a silted flocculent mud. Sometimes this tributary stream may be thickly forested with gallery forest along its whole length, or in scattered patches only.

M. The tributary then enters the main river which is usually very wide, swift and turbulent with rocky rapids and deep still pools; the volume of water may be enormous, and the water is often very turbid and red with suspended soil particles. Fringing reeds may be present in local patches.

O. The main river then enters a lake through a large or small papyrus swamp, of typical 'sudd' formation; or in the case of the easterly flowing rivers in Kenya, the river enters the sea through typical mangrove swamp.

N. If the lake is fresh water, the extensive open waters may beat upon a rocky or sandy foreshore, or in sheltered bays be fringed by dense papyrus sudd. The lake water is usually fairly clear, but is brown-stained and smelly in the papyrus swamp proper.

Q. Occasionally fairly large or small marshes of *Cyperus* or *Typha* reeds occur in a grazing area, unconnected with the main drainage channels and with no outflow; the water in such is turbid, stagnant and scummy with iron bacteria.

P. In some wider valleys and flat areas, independent waterholes may occur, from a few feet to several yards in diameter, unconnected with any drainage channels and differing markedly from habitat H in having no outlet trickle, being 'closed'. The bottom is usually muddy, the water deep or shallow and clear with fringing reeds and floating beds of *Pistia* (water lettuce) or turbid and soapy if used by natives for washing.

Cattle-grazing pastures in settled and native reserve areas may extend along both banks of the tributary and main river on to the lake shore, and watering of stock may be carried out at any of these habitats.

Occasionally the main river (or tributary) may not reach either a lake or the sea, but end in extensive swamps such as the Uaso Nyiro (northern) which loses itself in the Lorian Swamp during the wet season, or the Uebe Shibeli in Somalia. These swamps resemble habitat Q. Such rivers or tributaries if flowing through desert country like Turkana or the Northern Frontier District may not even reach a swamp but dry up before reaching an outlet during the dry seasons, leaving only disconnected pools in their course resembling habitat F, which may in turn also dry up. The Uaso Nyiro (northern) during the dry season and the Turkwell are examples of such.

Certain other well-defined aquatic habitats in Kenya have not been included in the above diagrammatic scheme, and will be dealt with now.

S. Trout streams. These are essentially an enlarged version of habitat B, extended down the valley to meet the main river. They are, in fact, small rivers, arising from typical seepage heads such as A, then flowing through bamboo, rain forest, dry forest and native reserve from about 10,000 to 6000 ft.; the water is usually clear, swift and turbulent with rapids, riffles, stiller pools and canal-like stretches; the bottom is rocky, silted in the deeper pools to form mud banks, and the river is anything from one to several yards wide.

T. Furrows. Occur in many areas, used for irrigation or water-supply purposes and led off from a trout river or habitat B; frequently with a mud bottom, clear water, a slow rate of flow and biologically similar to habitat D.

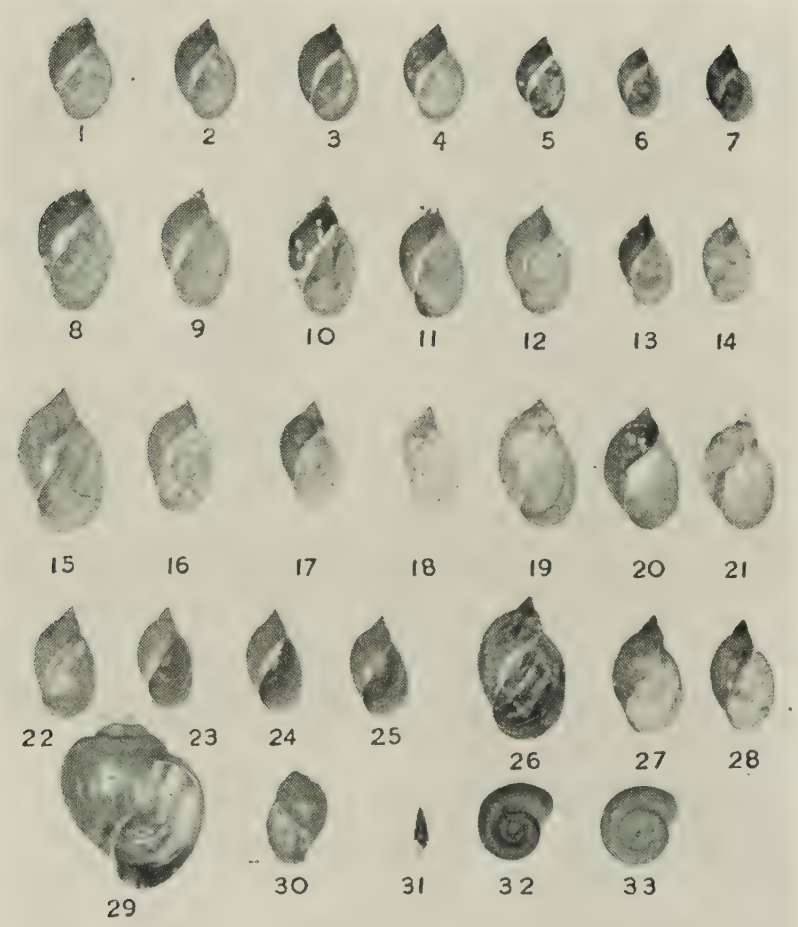
U. Ditches. Cut for drainage purposes and if with permanent water resembling habitat D (Pl. 7, photo 4).

V. Dams. Resemble small or large natural lakes, and are formed artificially by damming seepages and streams and often have no outflow. The water is often deep, shallower at the edges, and clear with floating vegetation such as *Nymphaea* or *Potamogeton* and emergent fringing reed beds. They may be very large in area (Pl. 8, photos 2, 3).

W. Deep wells. Distinguished from open waterholes such as P by being deep artificially sunk shafts to tap underground water. They occur in settled areas, in the Coast Province, and round Wajir in the Northern Frontier District.

X. Vleis or *mabuga*. Shallow grassy pans common in the highlands, which become flooded and marshy in the wet season, being dry for the remaining months of the year. If permanently flooded, they would evolve into habitat Q, since they seldom have a drainage outlet.

Y. Puddles and casual storm water. Small ephemeral collections of water at roadsides, on earth roads in car tracks, etc., usually drying a day or two after rain. Larger collections form the well-known temporary ponds, lasting for a month or two, which develop in a very short time after flooding a



Shells of *Lymnaea caillaudi* and associated species of molluscs.

Nos. 1–7. *Lymnaea caillaudi*. Canalized seepage, Lake Solai, Rift Valley, Kenya Colony.

Nos. 8–14. *Lymnaea caillaudi*. Irrigation furrow, Nanyuki, Kenya Colony. Eroded shells.

Nos. 15–18. *Lymnaea caillaudi*. Large dam, Ngong, Kenya Colony.

Nos. 19–21. *Lymnaea caillaudi*. Botha Falls, Marsabit, Northern Frontier District, Kenya Colony.

Nos. 22–25. *Lymnaea caillaudi*. Marshy stream, Hoey's Bridge, Kenya Colony.

Nos. 26–28. *Lymnaea caillaudi*. Marshy stream, Nyiribogi Valley, Central Kavirondo, Kenya Colony.

No. 29. *Pila* sp. Athi River, Kenya Colony. A small specimen.

No. 30. *Physopsis globosus*. Marshy stream, Kabete, Kenya Colony.

No. 31. *Bulinus forskalii*. Roadside ditch, North Kavirondo, Kenya Colony.

No. 32. *Biomphalaria pfeifferi*. Marshy stream, Kabete, Kenya Colony.

No. 33. *Biomphalaria sudanicus*. Seepage by Yala river, Central Kavirondo, Kenya Colony.

All natural size.

1. Seepage by Ugege river, Central Kavirondo, Kenya. Partly dammed for watering stock. Habitat C. *L. caillaudi* numerous, associated with *Pila* sp., *B. forskalii*, and *B. pfeifferi*. Infection rate nil. 17 Aug. 1944.

2. Drinking and washing pool by Luru river, Central Kavirondo, Kenya. Habitat H. *L. caillaudi* very abundant in clear water by *Pistia* and in axils of *Pistia* leaves. Associated with *B. pfeifferi* and *B. forskalii*. Infection rate nil. Lower soapy portion of pool (top right of picture) negative for snails. 19 Aug. 1944.

3. Shallow marshy portion of Mathari river, with slight flow. Habitat E. Kabete, Kenya Colony. *L. caillaudi* abundant, associated with *P. globosus* and *B. pfeifferi*. Infection rate 5 % *Fasciola*. May 1940

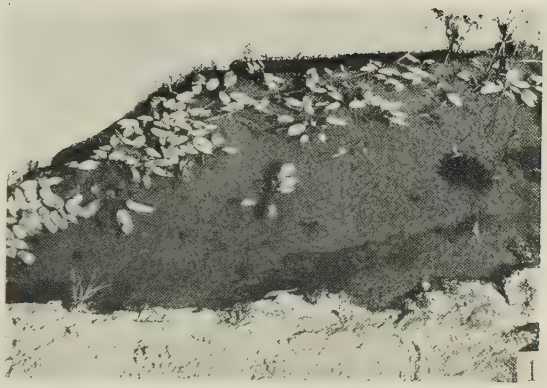
4. Shallow marshy portion of Pundu river, with slight flow. Habitat E. Central Kavirondo, Kenya Colony. *L. caillaudi* very abundant, associated with *B. pfeifferi*. Infection rate 12 % *Fasciola*. 26 Aug. 1944.

1. Seepage channels by Gaula river, Central Kavirondo, Kenya. Habitats C, D. The overgrown channel on the right negative for snails, the open channel on the left positive, with *L. caillaudi* very abundant, associated with *Pila* sp., *B. forskalii* and *B. pfeifferi*. Infection rate 12 % *Fasciola*. Dense reedy swamp in background negative for snails (Habita- Q). 21 Aug. 1944

2. Seepage channels by Sese river, Central Kavirondo, Kenya. Habitat D. The weedy channel on the right positive for snails, *L. caillaudi* being abundant, associated with *B. pfeifferi* and *Pila* sp. Infection rate nil. The cleared channel on the left negative for snails. In the background, deep reedy portion of the Sese river, negative for snails. Habitat L. 27 Aug. 1944.

3. Shallow trickling portion of Namunyiri river, North Kavirondo. Habitat E. A common watering place for cattle; note cattle droppings by water, bottom left of picture. *L. caillaudi* numerous, associated with *Pila* sp. Infection rate 41·7 % *Fasciola*. 13 Sept. 1944.

4. Stone-pitched ditch for flood and seepage water, Kabete, Kenya. Habitats U', D. Formerly *L. caillaudi* abundant, associated with *B. pfeifferi*. Infection rate 1·1 % *Fasciola*. At the time the photograph was taken the upper end of the ditch (bottom of picture) was very overgrown and both snails practically absent; smaller specimens were more abundant at the lower cleaner end (not well seen). In the background a stagnant swamp with ferruginous water, negative for snails. Habitat Q. Jan. 1945.



1. Relict rock pool by the side of a dam, Kabete, Kenya. Habitats G, V. *L. caillaudi* very scanty among *Potamogeton*, no associated snails. Infection rate nil. Bottom rocky, covered with algal 'mush'. March 1945.

2. Small water supply dam, Kabete, Kenya. Habitat V. Negative for *L. caillaudi* at time of photograph, these having all been stranded previously in flood pools above present level. Bottom rocky, covered with algal 'mush'. March 1945

3. Large artificial dam, Athi plains, Kenya. Habitat V. *L. caillaudi* very scanty among fringing vegetation (left of picture), absent on exposed shore (right of picture). March 1940

4. Channelled seepages by Mathari river, Kabete, Kenya Colony. Habitats C, D. *L. caillaudi* abundant, associated with *B. pfeifferi*. Infection rate 5% *Fasciola*. March 1940.

rich and diverse crustacean, rotifer, planarian and protozoan fauna of peculiar type laying drought-resistant eggs or forming drought-resistant cysts. Murram 'borrow pits' are a similar type of habitat, but if holding water permanently resemble habitat P.

Z. Artificial small bodies of water such as cattle troughs, cement tanks, rain-water tanks, etc.; these usually have no macrophytic vegetation.

AZ. Ornamental ponds in gardens, small and planted up with water lilies and other aquatic plants.

(*b*) *Habitat range*

The tolerance range in habitat is most noticeable in the dry season when the differences between the various habitats are sharply marked, and flood waters do not obscure the main features. It is essential when assessing the suitability of a habitat, that not only should the presence of the snail be taken into consideration, but also its abundance in that habitat. Obviously habitats which show only scanty numbers of individuals cannot be as favourable as others where the snails are abundant at the same time of the year, even though a greater number of the latter may be negative for snails.

Table 1 summarizes on this basis the habitat range of *Lymnaea caillaudi* in Kenya Colony during the dry season. These results are derived mainly from personal records in various parts of the Kenya

Table 1. *Summary of habitat types available for, and occupied by,* Lymnaea caillaudi *in Kenya Colony*

Series	Presence of snails	Habitat types	No. examined	No. with *Lymnaea caillaudi*
1	Abundant, 20–25 or many more individuals to the square yard	A. Clean seepage heads of streams	27	15
		C. Clean seepages at the sides of valleys	6	5
		E. Shallow flat portions of small streams	16	11
		H. Small clean water spring pools	7	4
		I. Outlet trickles from such pools	5	4
		T. Irrigation furrows	3	2
		D. Irrigation channels in *shambas*, not cleared	20	10
2	Scanty, 1–2 individuals per 10 sq. yd.	K. Small dams in a stream, if clear water	2	1
		V. Large open water dams, with clear water	3	3
		G. 'Relict' flood pools out of drainage course	4	4
		F. Intermittent stream valley with 'relict' pools	14	4
		J. Lower portions of streams with reed cut back	3	1
		N. Sheltered shores of large lakes	2	1
		AZ. Ornamental ponds in gardens	4	1
		L. Deep, mature portions of small streams	24	4
		B. Torrential portions of small valleys	7	1
3	Absent	M. Large main rivers	6	0
		O. Large dense papyrus swamps, stagnant water	1	0
		P. Closed turbid hillside pools, stagnant water	4 areas	0
		Q. Closed stagnant, reedy swamps	5	0
		S. Trout streams	7	0
		W. Deep wells	20	0
		X. Temporarily flooded vleis	4	0
		Y. Puddles and casual collections of storm water	Several hundreds	0
		Z. Small artificial collections of water such as cattle troughs and rain-water tanks	Several hundreds	0
		Also: any one of the Series 1 or 2 habitats if obviously polluted (in the widest sense), scummy, stagnant, impregnated with gas, much iron bacteria, soap, rubbish, etc.; or if heavily forested in deep shade; or with a swift rate of flow		

Highlands, and in the Central and North Kavirondo districts of Nyanza Province where habitats and habitat selection appear essentially similar. Owing to insufficient data and the fact that I have been unable to examine the areas myself, other records of snails sent in for identification purposes have been omitted from this table.

In general it may be said that all the habitats of series 1 are biologically similar in essential features, those of series 2 less so, and those of series 3 markedly different between themselves and from series 1 and 2.

One feature of this list is of considerable importance in connexion with the spread of fluke infection in any area. Since the preference of *Lymnaea* is for those habitats found mainly at the heads of valleys, the danger of infection spreading down the valleys during the wet season will be obvious. During periods of heavy rains when these valleys become flushed from the headwaters, the increased flow of water would tend to carry down from these headwater habitats large numbers of snails which may be infected; and the snails may also actively migrate downstream with the fresher water. Large numbers of viable freshly shed *Fasciola* cercariae would also be carried down, and on reaching quieter water downstream would encyst on the vegetation. At the same time the flooding of the banks would render available larger numbers of fluke miracidia from eggs in cattle dung dropped previously just above water-level.

It is, however, a common belief both among Europeans and natives concerned with the problem that fluke infection becomes intensified in cattle during the dry season. I have little data on the point, but this may well be so for several reasons. During the dry season when there is a general scarcity of good grazing, the cattle tend to fall off in condition and clinical fascioliasis becomes more evident; the cattle tend to graze nearer water for green grass and thus have more chance of becoming infected; during the dry season the vector snails are concentrated in these relatively small headwater habitats, this leading to a concentration of infecting miracidia and viable cercariae if such a seepage is used for watering stock; and lastly since the main breeding season of *Lymnaea caillaudi* is just after the long rains in July, there is a greater proportion of adult snails present in the dry season, January to March, and it has been found repeatedly that only the larger snails which are over 15 mm. long become infected with *Fasciola*, the larval stages being apparently unable to develop in smaller snails.

While the rainy season probably leads to a wide dispersal of light infections, the dry season intensifies the infection in a localized area. However, the time interval necessary for clinical symptoms to become evident is not known for *Fasciola gigantica* infection, but it is probably a short period only, since much of the damage results from the migration of the young flukes through the liver capsule.

Any valley producing vector snails only in its headwater habitats must inevitably be suspect for fluke for the whole of its length, although no snails may be obvious in its lower reaches. Unfortunately, there appears to be no exact information regarding the length of infective life of encysted *F. gigantica* cercariae, nor whether encystment is necessary before the cercariae are infective. It is probable, however, that at least the snails themselves either die out in the lower habitats when these become unfavourable during the dry season, or else actively migrate upstream to more suitable habitats.

4. THE HABITATS OF *LYMNAEA CAILLAUDI* IN OTHER PARTS OF AFRICA

Mozley (1944) classifies molluscan habitats in Southern Rhodesia as ephemeral streams, intermittent streams, (both my F), small perennial streams (my E), large perennial streams (my L and S), ponds (my G and P), small dams (my K), large dams (my V), underground waters, ornamental pools, swimming baths, water tanks (all my Z and AZ) and waters carrying industrial wastes. Unfortunately, however, neither the data for the snail collections made in Southern Rhodesia (Mozley, 1944) nor in Zanzibar and Tanganyika (Mozley, 1939) have been classified in accordance with this scheme by this author, but I have analysed his data as far as possible with the following results:

Zanzibar. 1 collection made in a pond (*Lymnaea*).

Tanganyika. 22 collections made (*Lymnaea*): 8 in streams; 4 in marshes; 4 in ponds; 2 in lagoons; 1 in a side channel of a river; 1 in a rice field; 2 in pools in a stream.

Southern Rhodesia. 331 collections made (*Lymnaea*): 139 in streams; 67 in rivers; 42 in dams; 17 in ponds; 5 in marshes in a stream; 2 in ditches; 37 in flood plain pools; 1 in a filter bed; 21 in pools at side of rivers.

It is difficult without further information to correlate these habitats with those of mine outlined above. It is probable though that Mozley's 'rivers' do not correspond to my habitat M, but to something of the type J or L, while 'streams' are probably of the nature of my E. It is clear, however, that Mozley's chief *Lymnaea* habitats are in general very similar to those in Kenya, in the possession of probably shallow, clean slow-flowing water with aquatic vegetation.

Dams occupy an important place also as a *Lymnaea* habitat; they are of peculiar interest in closely resembling running-water habitats as will be

explained below in the section relating to ecological factors (p. 180).

Mozley (1944) has also pointed out the importance of the stage of maturity, in the evolution of a pond, to its contained molluscan fauna. He classifies these as:

(1) A *juvenile*, or primitive stage, during which the pond contains a minimum of nutritive substances.

(2) An *intermediate* stage, during which food substances are present in abundance and waste products are not present in sufficient quantity to be detrimental to the growth or reproduction of living organisms.

(3) A *senile*, or evolved stage, during which food materials are present in limited quantity. In many instances there is an accumulation of plant or animal remains, or waste products which may be inimical either physically (by crowding) or physiologically (by poisoning) to living organisms.

With the reservation that food is by itself not the most important factor (others, such as dissolved oxygen, aquatic vegetation and so on being equally important, interacting and interdependent), this classification applies also to conditions in East Africa.

'Juvenile' waters are those such as small temporary pools, recently excavated borrow pits, etc., which, as in Southern Rhodesia, harbour mainly *Bulinus forskalii*. *Lymnaea*, *Physopsis* and *Biomphalaria* occur in the 'intermediate' types of waters, while the 'senile' evolved waters clearly correspond to my stagnant swamps such as Q, which are largely negative for molluscs. It is probable that the analogy can be carried a stage further, since such developmental stages can clearly be discerned in the diagram of a valley in Fig. 1, occupying positions in space rather than time; with the exception that the torrential habitat B would correspond to the 'juvenile' stage, where development is retarded by the swift current preventing the deposition of silt and consequent encroachment of vegetation into the water, which is the next logical developmental stage. My habitats A, C and E would correspond to the fertile 'intermediate' stage, and habitats L, Q, O, etc., to the 'senile' stage. Obviously the distribution of *Lymnaea* can be arranged in accordance with these stages, the snail being abundant in the 'intermediate' type of waters and scanty or absent in the 'juvenile' and 'senile' types.

In the Belgian Congo (Pilsbry & Bequaert, 1927), *L. natalensis undussumae* apparently prefers shallow pools in savanna country, or pools in rocks with plants, a muddy bottom rich in decaying vegetable matter, with quiet or semi-stagnant waters of small size. They may be found commonly in that country in shallow depressions in savanna country which may completely dry up after the rains, the molluscs either burying themselves deep in the mud, or surviving in the larger permanent ponds.

Such a habitat preference is very different from that in East Africa and Southern Rhodesia, and it may be due to a scarcity of favourable habitats of the East African type, or perhaps to a higher humidity and a more even, heavier rainfall favouring survival in such temporary collections of water. These snails may also occur in slowly flowing water in this region however, as these authors' records show.

5. ENVIRONMENTAL FACTORS INFLUENCING THE DISTRIBUTION OF *LYMNAEA CAILLAUDI* IN KENYA COLONY

The definition of the tolerance range of this vector snail has led to a study of the possible factors which influence its distribution, in an attempt to discover why some habitats should be more favourable than others.

(*a*) *Influence of* pH

Probably because it is so easily measured in the field, the hydrogen-ion concentration of the water in an aquatic habitat has always been a feature of the environment rather alluring to ecologists, some fresh-water ecologists believing they have found in it a factor of profound influence on aquatic animals, others discounting it altogether. The truth, as with so many ecological factors, probably lies half-way, since *p*H itself is of course bound up with many other factors such as the alkali reserve, salinity, free CO_2 and the amount and state of organic matter present in the water, any one or all of which may in themselves be determining factors. Welch (1935) gives a well-balanced summary of these aspects.

With particular reference to Lymnaeid snails Atkins (1923) and Atkins & Lebour (1923) first claimed its importance as a habitat indicator for *L. truncatula*, which they found occurring only in waters with a *p*H range of 6·4–7·8 (16 samples). Walton & Wright (1926) rather discounted the importance claimed for *p*H by Atkins & Lebour, showing that in 26 samples, all positive for *L. truncatula*, the *p*H range was 6·0–8·6. Økland (1936) recorded the same snail from a range of *p*H 5·6–8·6; Peters (1938) recorded a positive range of 6·9–8·2 for 22 samples; while Bertram (1939) found *L. truncatula* restricted to water of *p*H 7·3–7·7 on Inner Hebridean Islands. Hatzky (1940) found the optimum *p*H for this snail to lie between 7·0 and 8·0, though he showed that *p*H does not serve to differentiate the habitats of the various species of *Lymnaea* in Europe.

Boycott (1936) considered *p*H to be a rather doubtful factor, owing to the difficulty of interpreting field results, especially in relation to the calcium content

of the water, which may be more important. He concluded that its chief usefulness was merely the ability quickly to distinguish alkaline and acid waters in the field. It is not a major factor in snail distribution, and the word on the bottle—'Indicator', not 'Controller'—sums up its function best.

During this study, 133 aquatic habitats in the Lake Province and Highlands of Kenya have been examined with particular reference to *p*H, tests being made with B.D.H. Universal Indicator within 2 hr. of collection of the sample. Fifty of these habitats were positive for *Lymnaea caillaudi*, and the frequency distributions of the *p*H values for all waters and for the positive samples are shown in Table 2.

The results indicate that while *L. caillaudi* is apparently tolerant of a range of *p*H 6·0–9·5, it is more frequently present in the range *p*H 6·5–8·0; these values, as shown in the table, are in fact also the most commonly occurring in all waters positive or negative for snails. This range for positive values is very similar to those given for *L. truncatula* above.

shows that similar conditions may prevail in East Africa.

It is clearly difficult to relate the distribution of *Lymnaea* to a particular set of *p*H values, when one habitat alone may show a range from *p*H 6·5 to 9·5 during one day.

(b) Influence of total hardness of the water

The presence of calcium in the water is probably of more importance than *p*H, as Boycott remarks, since it is used in the construction of the shells, and probably dissolved lime salts also play some part in regulating the osmotic pressure of the snails' tissues. In addition, it may regulate the quality and quantity of aquatic vegetation and hence affect the snails indirectly.

There has been little work done in Africa on the importance of calcium salts to aquatic molluscs. Pilsbry & Bequaert (1927) state that the superficial waters of the Congo basin show 'a low concentration of lime', which may be responsible for the scarcity of molluscs in some parts, the profusion of snails in the

Table 2. *Frequency distribution of* Lymnaea caillaudi *in relation to* pH *of the water in positive and negative habitats*

*p*H ...	5·5	6·0	6·5	7·0	7·5	8·0	8·5	9·0	9·5	10·0
No. of all waters	2	12	27	20	19	35	14	1	2	1
No. of waters positive for *L. caillaudi*	0	3	12	8	10	12	3	1	1	0

Mozley (1944) has shown that *Physopsis globosus*, a common carrier of *Schistosoma haematobium* in East and South Africa, tolerates a *p*H range of 6·3–8·5, with an optimum of 7·3–7·5.

A small area in Marach location in the North Kavirondo district of Kenya Colony has waters which are all on the acid side (*p*H 6·0–6·5), and which are fairly densely populated by *Lymnaea caillaudi*, an unusual state of affairs. Collections from this area influence the above table, but have been included for the sake of completeness; there is a possibility, however, that these Sio drainage area *Lymnaea*, which also differ slightly in shell morphology, are on a cline from *L. caillaudi* (s.str.) as found elsewhere in Kenya. While therefore *L. caillaudi* (s.l.) appears to be tolerant of a wide range of *p*H, it is possible that excessive acidity or alkalinity (say *p*H 5·5 and below or 10·0 and above) may act as limiting factors, but such are probably rare in natural waters in East Africa.

As Boycott (1936) points out, the hydrogen-ion concentration of the water in any particular habitat may vary quite widely from hour to hour during the day, owing to gaseous interchange set up by aquatic plants during photosynthesis, with particular reference to the CO_2 content. Several examples of such variation are given by this author, and Table 9

great lakes of Africa perhaps being caused by the 'higher concentration of lime compounds due to active evaporation without much dilution by outflow'. These authors conclude that the generally thin, fragile and translucent texture of the African *Lymnaea* is evidently due to the scarcity of lime in the water in which they live. The beneficial action of calcium salts in the water, particularly calcium sulphate, on shell construction was shown long ago by Colton (1908).

Mozley (1944) points out that, in Southern Rhodesia, limestones have a very restricted range, and this is true also of the populated highland and Lake Province areas of East Africa; the majority of East African limestones are found only in the north-east desert parts of the colony. Mozley gives figures for the distribution of bilharzia vector molluscs in waters of varying hardness in Southern Rhodesia, but unfortunately does not specify in his table which 'degrees of hardness' are employed. On the assumption that these are English (Clark) degrees of hardness, he finds *Physopsis* commonest in water with 85·8 p.p.m. Ca or less ('soft water'), less common in water with 85·8–228·8 p.p.m. Ca and over ('medium hard' and 'hard' waters) while *Biomphalaria pfeifferi* occurs almost as frequently in all types. These figures would appear to indicate that

Rhodesian waters are far 'harder' than those examined in Kenya, as I have no records of waters harder than 200 p.p.m. Ca.

In Central and North Kavirondo and round the Nairobi area 102 examinations of aquatic habitats have been made to determine the total hardness of the water by a Winckler method modified for field use (potassium oleate-alkaline tartrate), the total hardness being expressed in terms of parts of $CaCO_3$ per million. Of these habitats, 45 were positive for *Lymnaea caillaudi*, and the frequency distributions of all waters and positive habitats is shown in Table 3.

Clearly *L. caillaudi* is tolerant of a wide range of hardness values, the lowest value in which it has been found being 8 p.p.m. $CaCO_3$. It is again commonest in the most commonly occurring values, but probably has a lower limit of toleration somewhere about 8 or below which is a rather 'soft' water by any scale.

The influence of water hardness on shell formation is very noticeable when dissecting *Lymnaea* for infection rates, those from water about 8 to 20 p.p.m. $CaCO_3$ having brittle shells easily cracked on slight pressure, those from water of values above these having harder shells, usually with a cleaner, brighter surface, which require considerable pressure to crack.

Table 3. *Frequency distribution of* Lymnaea caillaudi *in relation to total hardness of the water in positive and negative habitats*

$CaCO_3$ parts per million ...	1–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–200
No. of all waters	7	42	16	14	6	7	1	1	2	3	3
No. of waters positive for *L. caillaudi*	3	18	5	8	2	4	0	1	0	2	2

(c) *Influence of water colour and type*

Stability of the water environment, in its widest sense, appears an essential feature for the presence of the snails, though difficult to express numerically. Thus in Kenya, *Lymnaea* does not occur in temporary puddles, marshes which dry up, or in any place where the current is above a certain (undetermined) minimum speed, or where the water-level is subject to violent fluctuations as in the torrential portions of streams, trout rivers or large main rivers. Similarly also, where the water is more or less violently disturbed by wave action as at the exposed shores of lakes, *L. caillaudi* is absent. Cleanliness of the water, i.e. freedom from suspended or colloidal silt and organic or inorganic fouling, is also necessary, as is a measure of shallowness, except in large dams. A slight current is favourable.

A swift current of water would obviously tend to dislodge a somewhat bulky organism like *L. caillaudi* in spite of its broad foot, organisms living in such an environment all being flattened, stream-lined forms such as some of the Ephemeroptera, or the Ancylidae amongst the molluscs. The absence of Lymnaeidae in temporary habitats, at least in Kenya, is probably due to their low resistance to desiccation (Cawston, 1929; Porter, 1938) and the generally low, dry-season humidity over the highland areas of Kenya Colony.

An interesting feature of many aquatic habitats in East Africa is the occurrence of heavy red flocculent precipitates of iron salts on the bottom, and if the water is stagnant, a scummy dirty appearance with an iridescent surface film. This appearance is very common in stagnant marshes, but is also quite frequent in ponds, streams, ditches and sometimes the quieter parts of large rivers. According to Ellis (cited by Pilsbry & Bequaert, 1927) it is due to a brownish coat of iron hydroxide being deposited by the action of bacteria belonging to the genera *Cladothrix*, *Spirophyllum*, *Siderocapsa*, *Leptothrix*, and *Crenothrix*, which also form the brown flocks or strings seen in the water. These bacteria absorb ferrous carbonate in solution in the water and re-deposit the iron later as ferric hydroxide. The bacteria occur chiefly in ground waters and only grow with rapidity when dissolved oxygen is lacking or almost so, and when the special salts which they precipitate are present. These two conditions are absolutely necessary, and the presence of much organic matter, absence of light, and the presence of carbonic acid in the water are favourable conditions also.

Such types of waters are of very great importance in East Africa because they are almost invariably negative for the aquatic disease-carrying animals such as *Anopheles* larvae, bilharzia vector snails and *Lymnaea caillaudi*. The latter I have found in such habitats only in the Marach location of North Kavirondo, whose peculiarities have been mentioned previously.

An important contribution to the study of the biology and chemistry of these ferruginous waters has recently been made by Williamson (1944), with particular reference to the absence of malaria-carrying mosquitoes in them. This author gives a full discussion of the chemical aspects, and concludes that, from the biological point of view, such waters are not inimical to mosquito larvae by virtue directly of their chemical constitution, but because of the inimical effects of colloidal iron on the growth

of algae, Protozoa and other micro-organisms which form the food of such larvae. Mosquito larvae, newly hatched from the egg, are unaffected by such iron-containing waters provided they are fed; but when placed in samples of such waters without added food, the larvae soon die of starvation. There is no evidence that the iron-containing iridescent surface films will suffocate the larvae. The characteristic absence of water insects, worms, Crustacea and Lymnaeid snails in such water is probably due also to the same cause, as most of these are directly dependent on microflora and microfauna for food. A few detailed observations round Kabete tend to support this view (see p. 193), and in Kenya such waters have been found invariably to have a distinctly acid *p*H of 5·0–6·5.

The presence of *L. caillaudi* in large dams as opposed to small stagnant pools and permanent puddles is clearly due to the effect pointed out by Boycott (1936) in dams and lakes, where 'the effective occupied [by snails] volume of water is therefore in contact with a larger, often much larger, volume of what may be called "free water", and this is of some importance in promoting cleanliness and diluting the products of activity and decay. Large loci of good depth are in this way equivalent to running water....' Such large bodies of relatively still water are therefore, as this author points out, often favourable habitats for typical running-water organisms of many types (not only molluscs), and hence the presence of *L. caillàudi*, a type also favouring moving water, in large dams where conditions apart from the actual physical current tend to be similar as in moving water.

(*d*) *Influence of dissolved oxygen*

The preference of *L. caillaudi* for those habitats having clean, trickling shallow water with a certain amount of aquatic vegetation suggests that the oxygen tension of the water may be an important factor in determining its distribution, since such places are usually saturated or supersaturated with oxygen; so also, of course, are habitats such as trout streams, but here the actual physical force of the current is the limiting factor.

L. caillaudi is a pulmonate mollusc, provided with a lung, which has only secondarily returned to an aquatic environment. As such, it is in the fortunate position of being able to use both atmospheric oxygen and oxygen dissolved in the water. Specimens in an aquarium are often seen with a bubble of air at the pneumostome, and the partly amphibious habit of *L. caillaudi* (individuals often being found a short distance out of the water on mud or reeds) is probably accounted for by this ability to use atmospheric oxygen. While under water they may also utilize the bubbles of oxygen present on the surface of aquatic plants (Pilsbry & Bequaert, 1927; Bequaert, 1928). At the same time, however, cutaneous respiration also occurs while under the water as pointed out by Pauly as long ago as 1877 (Pauly, 1877, cited by Pilsbry & Bequaert). Laboratory experiments have shown that such cutaneous respiration is measurable, and it is probably of considerable importance.

Even for atmospheric respiration via the lung, moisture is essential, otherwise *L. caillaudi* should be able to withstand much longer periods of desiccation; a film of moisture over the surface of the lung would be necessary for gaseous interchange as in mammals. *L. caillaudi* appears to be incapable of retaining such moisture in its lungs for long and, having returned to an aquatic environment, is obviously now more dependent on external water than in its previous evolutionary stage on land. Most freshly collected *Lymnaea* have air in their pulmonary cavity and float easily in water when the foot is not applied to a solid surface. In aquaria, snails often change their position in the water by releasing their hold on the substratum, floating to the surface and swimming on the surface film (or presumably being carried by the current in a natural habitat). When, however, such lung-enclosed air is used up as in a closed container, the snail sinks and the pulmonary cavity is seen to be filled with water; but respiration can continue in such a condition for several hours, indicating the use of oxygen dissolved in the water. The snail is probably incapable, however, of existing solely upon atmospheric oxygen, but if at any time it should evolve back on its tracks as it were and reattain the ability to keep its lungs moist over lengthy periods of time, it would become a much more dangerous mollusc than it is, because it would then be able to colonize many places now denied to it, owing to its partial dependence on dissolved oxygen.

(1) *Oxygen suffocation limit*

A series of experiments has been carried out to determine the lowest dissolved oxygen tension at which *L. caillaudi* dies of suffocation.

The technique in all these experiments was the same, one or more snails with shells cleaned as far as possible from algae and mud being enclosed in 300 c.c. of pure water of known oxygen content and *p*H, and kept for varying lengths of time until the snail was observed to be either in distress or dead (death being determined by the inability to recover when replaced in well-aerated pure water with a free air surface for 24 hr.). Temperatures were room temperatures in the laboratory, varying from 18 to 22° C. during the experiments.

The snails were either enclosed in stoppered bottles, closed carefully to exclude air bubbles and

Table 4. *The oxygen suffocation limits of* Lymnaea caillaudi

Exp.	no.	No. of *Lymnaea* in bottle	Method (S.=stoppered)	Start				Period of exp. (hr.)	Finish				Apparent O_2 used per hour per snail	Remarks
				Temp. ° C.	*p*H	O_2	% sat.		Temp. ° C.	*p*H	O_2	% sat.		
1	A	4	Under oil, aerated control	19·5	—	7·27	95·6	23	18·0	—	6·8	—	—	All four snails alive at end
	B	0	Under oil, non-aerated, blank control	19·5	—	7·27	95·6	23	18·0	—	7·2	—	—	
	C	1	Under oil	19·5	—	7·27	95·6	23	18·0	—	2·0	25·2	0·23	Snail alive at end
	D	2	Under oil	19·5	—	7·27	95·6	23	18·0	—	1·04	13·1	0·14	All snails alive at end
	E	4	Under oil	19·5	—	7·27	95·6	23	18·0	—	0·24	3·2	0·08	All snails alive at end
2	A	4	S., aerated control	21·0	5·5	7·1	96·0	24	21·0	7·0	5·23	—	—	All snails alive at end
	B	1	S.	21·0	5·5	7·1	96·0	24	21·0	5·5	1·38	18·6	0·24	Snail alive at end
	C	1	S.	21·0	5·5	7·1	96·0	24	21·0	5·5	2·06	27·8	0·21	Snail alive at end
	D	2	S.	21·0	5·5	7·1	96·0	24	21·0	5·5	0·69	9·3	0·14	Both distressed but alive, recovered in fresh water
	E	4	S.	21·0	5·5	7·1	96·0	24	21·0	6·0	0·53	7·1	0·07	2 snails dead, 2 motionless, recovered in fresh water
	F	4	S.	21·0	5·5	7·1	96·0	24	21·0	6·0	0·52	7·0	0·07	2 dead, 2 motionless, recovered in fresh water
3	A	2	S., aerated control	18·5	6·0	7·3	93·6	26	20·0	7·5	6·8	—	—	Both snails alive at end
	B	1	S.	18·5	6·0	7·3	93·6	26	20·0	6·0	4·3	56·8	0·12	Just alive at end, slight recovery in fresh water, then died
	C	1	S.	18·5	6·0	7·3	93·6	26	20·0	6·0	4·3	56·8	0·12	Motionless at end, recovered in fresh water
4*	A	2	S., aerated control	21·0	5·5	6·93	93·5	48	20·0	7·5	6·92	—	—	Both snails alive at end
	B	1	S.	21·0	5·5	6·93	93·5	48	20·0	6·0	2·08	27·5	0·1	Alive at end, very inactive during experiment
	C	1	S.	21·0	5·5	6·93	93·5	48	20·0	6·0	2·58	34·2	0·09	Alive at end, very inactive during experiment
	D	1	S.	21·0	5·5	6·93	93·5	48	20·0	6·0	2·77	36·6	0·09	Alive at end, very inactive during experiment
	E	2	S.	21·0	5·5	6·93	93·5	48	20·0	6·0	0·52	6·9	0·07	1 snail alive, 1 dead. Very inactive during experiment
	F	2	S.	21·0	5·5	6·93	93·5	48	20·0	6·0	0·69	9·1	0·07	1 snail alive, 1 dead. Very inactive during experiment
5	A	2	S., aerated control	19·0	5·5	7·62	99·0	48	19·0	7·5	7·1	—	—	Both snails alive at end
	B	1	S.	19·0	5·5	7·62	99·0	28	20·5	6·0	2·25	30·0	0·19	Snail in distress after 24 hr., recovered in fresh water
	C	1	S.	19·0	5·5	7·62	99·0	28	20·5	6·0	3·26	43·5	0·16	Snail in distress after 24 hr., recovered in fresh water
	D	1	S.	19·0	5·5	7·62	99·0	48	19·0	6·0	1·38	17·9	0·13	Snail distressed, but recovered in fresh water
	E	2	S.	19·0	5·5	7·62	99·0	48	19·0	6·0	0·69	8·9	0·07	Both dead, no recovery in fresh water
	F	2	S.	19·0	5·5	7·62	99·0	23½	19·0	6·0	2·94	38·2	0·09	1 died, infected with Xiphidiocercariae. Other infected *Fasciola* still alive
6	A	2	S., aerated control	20·5	5·5	7·27	97·0	48	21·0	7·5	6·75	—	—	Both snails alive at end
	B	1	S.	20·5	5·5	7·27	97·0	48	21·0	6·0	0·35	4·7	0·14	Dead, no recovery in fresh water
	C	1	S.	20·5	5·5	7·27	97·0	48	21·0	6·0	0·86	11·6	0·13	Alive at end
	D	1	S.	20·5	5·5	7·27	97·0	48	21·0	6·0	0·17	2·3	0·15	Dead, no recovery in fresh water
	E	1	S.	20·5	5·5	7·27	97·0	48	21·0	6·0	0·17	2·3	0·15	Motionless, recovered in fresh water
	F	2	S.	20·5	5·5	7·27	97·0	48	21·0	6·0	0·35	4·7	0·07	Motionless, both recovered in fresh water
7	A	2	S., aerated control	19·0	6·0	7·1	92·5	72	19·0	8·0	6·3	—	—	Both snails alive at end
	B	1	S.	19·0	6·0	7·1	92·5	72	19·0	6·0	0·69	8·9	0·09	Alive at end
	C	1	S.	19·0	6·0	7·1	92·5	72	19·0	6·0	1·3	16·9	0·09	Alive at end

*. Snails used in this experiment had been kept isolated in 3 × 1 in. tubes for 5 days previous for other purposes. All other snails used in the experiments were collected straight from a natural habitat an hour or less previously.

sealed with vaseline, the seal being broken at the end of the experiment and the water transferred carefully and quickly without agitation to titration bottles of known capacity; or else the water containing the snail was sealed with a ½ in. layer of pure paraffin, at the end of the experiment the snail being carefully withdrawn from below the paraffin and a sample portion of the water being withdrawn from below the seal for titration after fixation of the dissolved oxygen by the reagents introduced through the paraffin. No significant difference was apparent between the results from the two methods, but the paraffin-seal method proved more unreliable over long periods owing to the snail attempting to crawl through the paraffin during the experiments.

The dissolved oxygen determinations were carried out according to a standard Winckler procedure (Public Health Association, America, 1936), using manganous chloride, KOH-KI solution, but *N*/10 sodium thiosulphate.

As controls, two or more snails were kept under constant aeration in similar bottles containing a similar portion of the known oxygen content water. All bottles during the experiments were kept in shaded conditions not exposed to strong light at any time, nor yet in complete darkness.

The oxygen percentage saturation results are calculated on the temperature measured at the time of determining the dissolved oxygen, allowing for the reduced atmospheric pressure of the altitude at which the experiments were carried out (Kabete, altitude 6200 ft.).

The experiments were carried out over 24–72 hr. periods, and Table 4 summarizes the results, oxygen being expressed as parts per million of oxygen, as well as percentage saturation.

It is clear from these results that the oxygen-lack death-point may vary widely with individual snails, but in general a percentage saturation of 9% or under leads to death, though the four snails in Exp. 1 E were still alive after 23 hr. when the oxygen tension had fallen to 3·2% saturation. What is also clear from the observations, however, is that below about 40% saturation the snails begin to exhibit signs of distress—these being noted as a contracted, motionless appearance on the bottom of the vessel, or feeble movements of the foot and tentacles while the snail lies upside down on the bottom; normally a snail placed upside down in fresh oxygenated water is able to right itself within a few minutes by vigorous elongated stretching of its body outside the shell till the bottom is touched. The true 'immediate' death-point of a snail is very difficult to determine by simple observation.

There is an indication in Exp. 5 F that a trematode-infected snail may have a very high oxygen death-point. This snail was found heavily infected with a species of Xiphidiocercaria common enough at Kabete; but it should also be noted that another snail in the same vessel infected fairly heavily with *Fasciola* was still alive at this point.

That the deaths observed were not due to starvation is shown by the controls, and in fact *Lymnaea caillaudi* appears to be able to exist for several days without obvious food. Though the size of the snails experimented upon was not determined for this series of experiments, the size of the snail influences its oxygen consumption as shown in the next section.

Such experiments, of course, are unnatural in so far as the snail is being subjected to a gradually decreasing oxygen tension caused by its own metabolism in a closed volume of water, and to an increasing concentration of its own waste products; such a state of affairs probably does not occur in nature, and the results therefore merely indicate in general the percentage saturation values below which distress or suffocation may occur. It is possible that were a snail to be subjected to a *constant* oxygen tension of say 40% saturation, it would die much sooner than one subjected to say a constant 80% oxygen saturation; such conditions, however, are very difficult to reproduce satisfactorily in the laboratory owing to the inevitable usage of the dissolved oxygen by the snail and the difficulty of replacing it in the water at an exactly equivalent rate to maintain a constant saturation value of 80% or lower. Probably in nature it is the *duration* of exposure to low saturation values which determines the absence or death of snails in any particular habitats, this having its main effect on reducing the activity of the snail necessary for feeding or other movements and reproduction.

(2) *Oxygen consumption*

The oxygen consumption rates recorded in Table 4 are noted as 'apparent' only, since obviously they are an average consumption per hour per snail during the experiments, and do not necessarily indicate that the snail is using the dissolved oxygen at an even rate.

A curious anomaly is, however, apparent in these experiments, whereby an isolated individual snail *appears* to use oxygen at a faster rate per hour than the individuals of two snails kept together, and the individuals of two snails kept together *appear* to use oxygen at a faster rate per hour than the individuals of four snails kept together. This finding is very similar to that of Valente (1943) for the crab *Trichodactylus petropolitanus*; this worker concluded that the isolated crab uses oxygen at a greater rate than do groups of four crabs; and that two crabs used more than four. The result, however, for *Lymnaea caillaudi* is fallacious, as is clearly shown by

testing the oxygen consumption of individuals and groups over a much shorter period of time; results of such an experiment are shown in Table 5.

A further point noted from the table is that during such a short period of time, the oxygen consumption per hour per snail is markedly greater than for individual snails in the 24–72 hr. experiments. This suggests that the oxygen consumption of individual *L. caillaudi* in a closed container is not constant, but decreases with decreasing oxygen tension of the water. If such was the case, an explanation of the anomaly evident in Table 4 would at once be apparent, since two or more snails in a closed volume of water would clearly cause the oxygen tension of the water to fall to a much lower level than would one snail in the same period of time, and the 'average' consumption per snail of these two or more snail groups would show a corresponding decrease, when compared with the 'average' consumption of an isolated snail for the same period of time.

snail of group E died and was found heavily infected with Xiphidiocercariae, so another snail of approximately the same size and infected equally heavily with *Fasciola* was added to the remaining snail of this group for the 16-hourly and subsequent periods. In constructing the graphs the percentage saturaton of oxygen of the water for the 3-hourly period has been corrected to a starting figure of 95%, the approximate average for all the other periods at commencement, because on testing the water subsequent to starting this 3-hourly set it was found that the water had been insufficiently aerated; beyond smoothing the percentage saturation curve, the correction does not alter the consumption curves appreciably.

As before, the consumption figures are, of course, the average oxygen consumption per individual per hour over the period of the hours tested; hence the *actual* consumption of oxygen by an individual during say the forty-eighth hour would be less than

Table 5. *The oxygen consumption of isolated and grouped* Lymnaea caillaudi *over a short period of time*

No. of *Lymnaea* in bottle	Method	Start O_2	Period of exp. (hr.)	Finish O_2	O_2 loss	O_2 per hour per snail
1	Stoppered	7·1	3	6·15	0·95	0·32
1	Under oil	7·1	3	5·6	1·5	0·5
2	Stoppered	7·1	3	5·02	2·08	0·34
2	Under oil	7·1	3	4·8	2·3	0·38
4	Stoppered	7·1	3	3·19	3·91	0·32
4	Under oil	7·1	3	3·6	3·5	0·3

This hypothesis has been tested by determining the oxygen consumption of individual snails isolated singly and in groups of two over successively increasing periods of time.

The technique employed was as before, the snails being enclosed in water of known oxygen content in stoppered bottles sealed with vaseline, the seal being broken and the water tested at the end of each experimental period. At the end of each experiment the snails were isolated singly in marked 3 × 1 in. tubes in which the water was changed every day, fresh fully oxygenated water being added each time, together with an abundance of mud containing diatoms and other algae, and a few rotting reed leaves covered with an algal film for food. In these tubes the snails were allowed to recover and feed for at least 24 hr. before subjecting them to the next experimental period.

After death, the shells were measured and the snails examined for infection with larval trematodes. The results of the experiments are recorded in Table 6 and shown in Figs. 2–4.

Two points in connexion with these results should be noted. At the end of the 6-hourly period, one

the figure calculated, and this would be particularly marked during the hour of death, a point which, as has been explained previously, is very difficult to determine for these snails. The oxygen is recorded in parts per million, and percentage saturation values are calculated on the water temperature at the beginning of the experiments, for an altitude of 6200 ft.

The following points are apparent from the figures and graphs:

(1) All the individuals, whether isolated or in groups of two, show an initial rise from a low figure to a maximum consumption at 2 hr., followed by a decrease in the consumption rate. This rise I believe to be due to the change over from partly atmospheric respiration to wholly aquatic respiration. On the introduction of the snails at the beginning of each period to the water in the bottles before closure, the snails invariably floated, indicating the presence of air in the pulmonary cavity, and the explanation of this rise probably lies in the fact that after about 2 hr. in a closed container this air seemed to be used up and the snail commences using the oxygen dissolved in the water. The rise may be apparent

Table 6. *The oxygen consumption of* Lymnaea caillaudi

Duration of exp. in hr.	Start: Temp. ° C.	Start: *p*H	Start: O_2 p.p.m.	Start: % sat.	Snail	Finish: O_2 p.p.m.	Finish: % sat.	Finish: Average % sat.	O_2 per hr. per snail	Average O_2 per hr. per snail	Remarks (+ + + = ¾ of liver destroyed by larval flukes)
1	19·0	6·5	7·45	97·0	A	7·38	96·0	95·0	0·07	0·143	
					B	7·27	94·5		0·18		
					C	7·27	94·5		0·18		
					D (2)	7·24	94·0	93·5	0·105	0·125	
					E (2)	7·16	93·0		0·145		
2	19·0	5·5	7·38	96·0	A	7·0	91·0	90·3	0·19	0·213	
					B	6·93	90·0		0·225		
					C	6·93	90·0		0·225		
					D (2)	6·76	88·0	86·5	0·155	0·181	
					E (2)	6·55	85·0		0·207		
3	20·0	5·5	6·76	89·5	A	6·35	84·0	83·0	0·137	0·159	
					B	6·23	82·5		0·177		
					C	6·27	83·0		0·163		
					D (2)	6·03	79·8	78·0	0·124	0·147	
					E (2)	5·74	76·0		0·17		
4	18·8	6·5	7·37	94·5	A	6·87	88·0	87·3	0·125	0·138	
					B	6·79	87·0		0·145		
					C	6·79	87·0		0·145		
					D (2)	6·48	83·0	81·0	0·112	0·133	
					E (2)	6·14	78·5		0·154		
6	18·8	6·5	7·62	98·0	A	6·87	88·0	87·0	0·125	0·138	Distressed. Recovered in fresh water
					B	6·75	86·5		0·145		Distressed. Recovered in fresh water
					C	6·75	86·5		0·145		
					D (2)	6·55	84·0	81·0	0·089	0·109	Distressed. One recovered in fresh water; other died
					E (2)	6·08	78·0		0·129		Distressed. Recovered in fresh water
8	19·8	6·0	7·27	95·5	A	6·35	83·5	82·0	0·115	0·128	
					B	6·23	82·0		0·13		Distressed. Recovered in fresh water
					C	6·16	81·0		0·139		
					D (2)	5·93	78·0		0·084		Single snail only, distressed. Recovered in fresh water
					E (1)	5·84	77·0		0·18		Motionless. Recovered in fresh water
16	22·2	6·5	6·93	95·0	A	5·67	78·0	75·0	0·079	0·094	
					B	5·09	70·0		0·115		Motionless. Dead
					C	5·54	76·0		0·087		
					D (2)	4·48	61·5	50·0	0·077	0·102	Further snail of approx. same length added, infected *Fasciola* + + +
					E (2)	2·87	39·4		0·127		
24	19·5	6·5	7·27	95·5	A	5·67	74·5	70·0	0·067	0·081	
					B	5·02	66·0		0·094		
					D (2)	4·09	54·0	40·0	0·067	0·089	
					E (2)	1·9	25·0		0·112		
48	19·9	6·0	7·27	95·5	A	4·65	61·4	53·3	0·055	0·068	Motionless. Recovered in fresh water
					B	3·43	45·2		0·08		
					D (2)	1·73	22·8	14·2	0·058	0·065	Motionless. Both dead
					E (2)	0·42	5·5		0·072		
72	19·9	6·0	7·27	95·5	A	3·88	51·0	43·6	0·046	0·055	Dying. Died 1 hr. after in fresh water
					B	2·75	36·2		0·063		Motionless. Dead
					D (2)	0·35	4·6		0·048		Motionless. Both dead

only and not actual, and the consumption may be at an even rate, since naturally respiration of air enclosed in the pulmonary cavity would not be measured by the fall in oxygen content of the water. It is interesting, however, that even after 1 hr., *some* oxygen in the water is being used, though the snails still floated when the bottles were opened, indicating that the snail is probably not entirely independent of dissolved oxygen even under natural conditions. After 2 hr., on opening the bottles, the snails invariably sank, indicating that the pulmonary cavity was no longer filled with air.

(snail C). This is true both for isolated individuals and for the average individual in each group of two snails. Up to 8 hr. at least, the consumption of the smaller snails is greater relative to size than that of the larger snails (as measured by length), and such would be expected if respiration was mainly cutaneous, since the smaller the animal the greater the surface area in relation to its volume. The relative proportions are difficult to calculate accurately, since the true surface area of a convoluted body such as that of a snail is almost impossible to calculate from shell dimensions only.

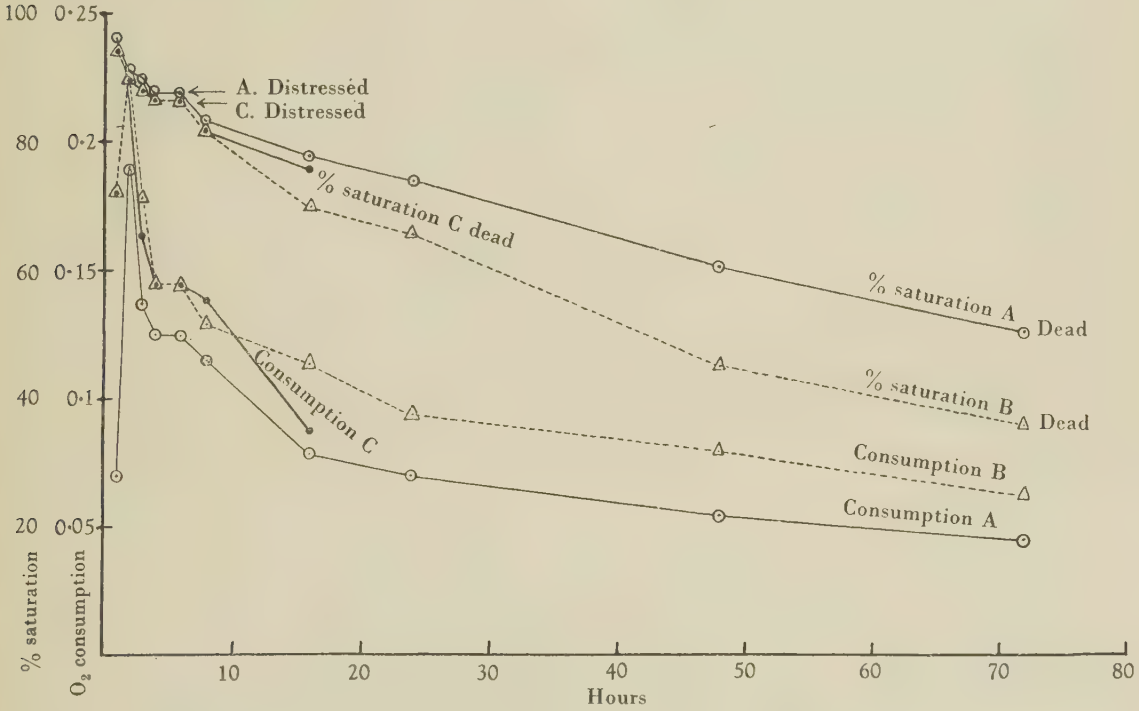


Fig. 2. Oxygen consumption (p.p.m. per hr.) of isolated individual *L. caillaudi*.

(2) After this initial rise, the graphs show that oxygen consumption of individuals does not remain constant, but decreases as the percentage saturation of the water decreases, until death supervenes. This decrease is rapid to saturation values of 75–85 % and thereafter is much more gradual for all individuals, though there does not appear to be a fixed proportional relationship between saturation value and oxygen consumption; the higher the rate of consumption the greater the decrease in saturation value of the water, but this greater decrease does not lead to a proportionate lowering of the consumption rate.

(3) Reference to the sizes of the snails tested (Table 7) also shows that the larger the snail (as measured by length) the higher is the consumption rate in all cases except when death supervenes early

(4) In all cases except the doubtful snail C, the larger snails died first, probably of suffocation, because their absolutely greater rate of consumption lowered the saturation value to suffocation point quicker than the smaller snails. In Fig. 2, although snail A is recorded as dead at the end of the 72 hr. period, it actually died about 1 hr. after transference to fresh water and must have been just on the point of death at the close of the experiment, whereas the larger snail B was definitely dead at the close of this 72 hr. period.

Considerable variation is apparent in the saturation-value death-point. For the two groups of two snails, death supervened at a saturation value of below 10%, for the isolated individuals death supervened at much higher values. It is possible

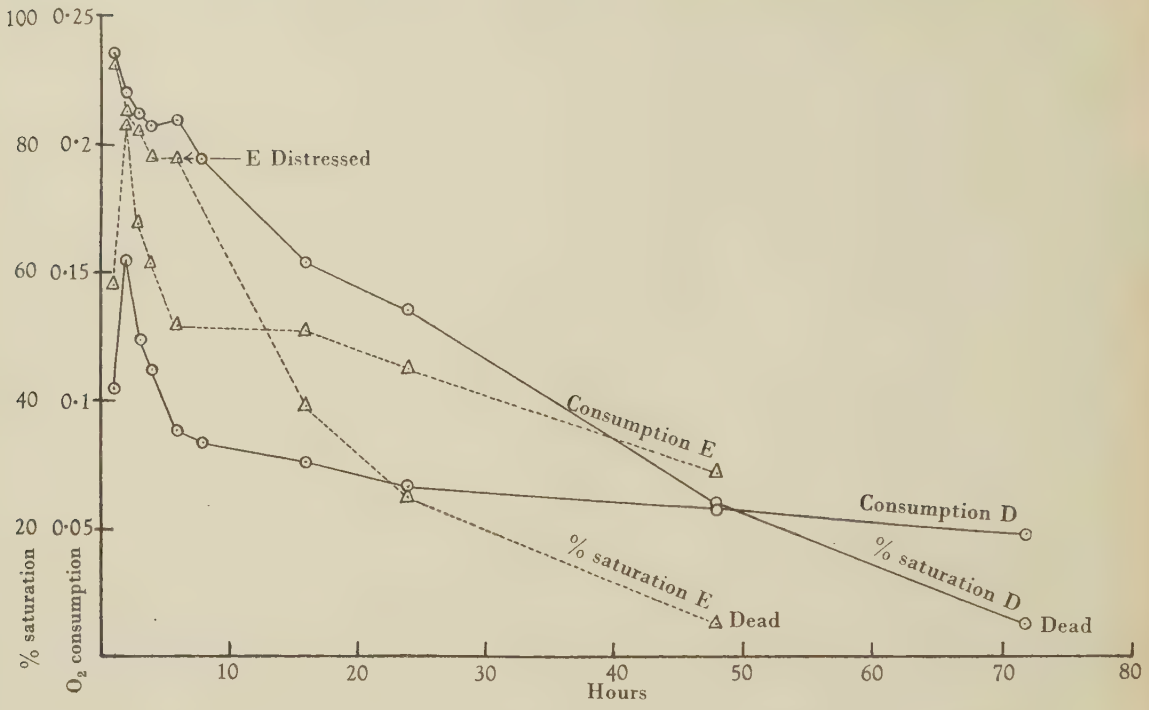


Fig. 3. Oxygen consumption (p.p.m. per hr.) of individual *L. caillaudi* isolated in groups of two individuals each (groups D and E).

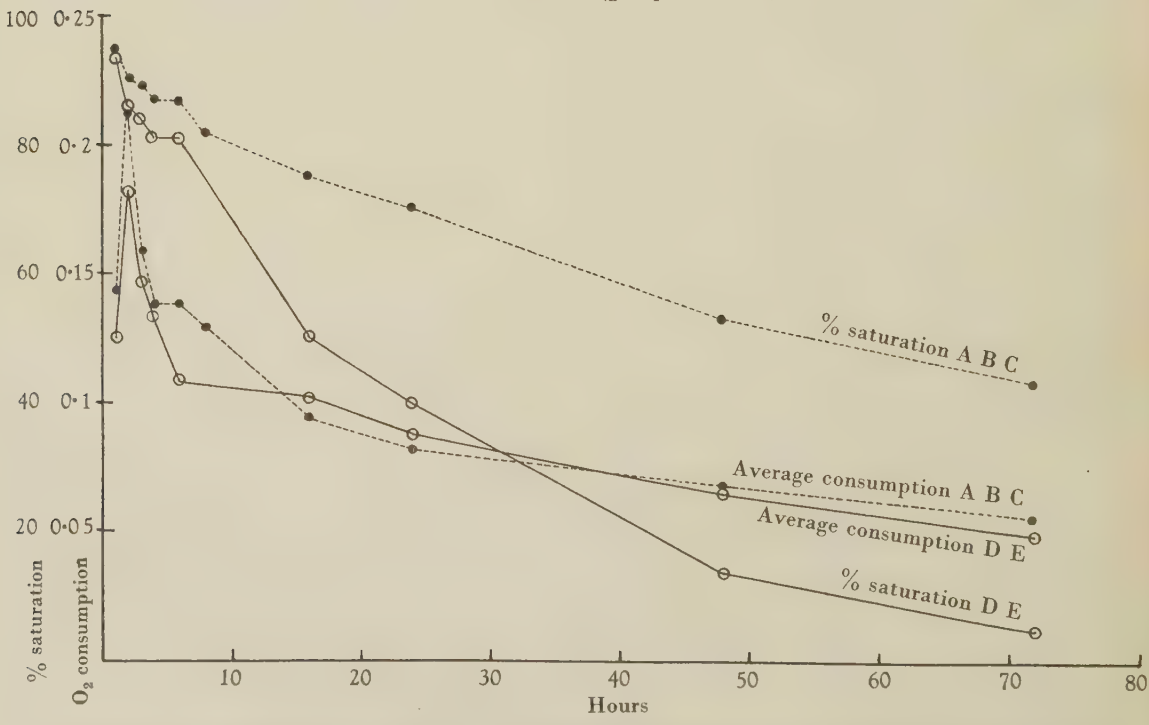


Fig. 4. Oxygen consumption (p.p.m. per hr.) of *L. caillaudi*, averaged for single isolated individuals (A, B, C) and for individuals isolated in groups of two each (D, E).

that over a prolonged period of time such as 72 hr., death for isolated individuals may be hastened at a high saturation value by other factors, such as a low *p*H.

(5) It is suggestive that the individual of group E infected with Xiphidiocercariae died so quickly, while its replacement infected with *Fasciola* died no sooner than its uninfected partner (cf. Table 4, Exp. 5 F).

(6) The high saturation values at which distress became evident are noteworthy, and are more reliable than those recorded in Table 4, where the experiments were designed for another purpose, and distress may actually have been evident some time before the experiments ended.

It is noticeable from the graphs that it is at such distress values that the oxygen consumption starts faster rate than do single isolated individuals, and hence their oxygen consumption is decreased in a correspondingly shorter period of time. As will be seen from Table 7, the average dimensions of snails A, B, C correspond very closely with the averages of the four snails in groups D and E, but obviously at any time up to 13 hr. the consumption of the individuals in groups D and E would appear to be much lower than A, B, C over the same period of time. Thereafter, in spite of the greater decrease in saturation value of the water in groups D and E, the oxygen consumption of both single and 'doubled' snails remains much the same. The group effect is due to a time factor, and progressive decrease of oxygen consumption rate, accelerated in the groups.

A probable source of error in any such experiments with molluscs is the production of oxygen by

Table 7. *Measurements (in mm.) of snails* (Lymnaea caillaudi) *used in oxygen consumption experiments*

Snail	*L*	*W*	*B*	*I*	*b*	Infected (+++ = ¾ of liver destroyed by larval flukes)
A	15·0	13·3	7·5	11·1	6·1	0
B	19·6	17·0	10·9	14·2	7·9	0
C	20·5	18·7	10·9	15·3	8·6	0
D 1	17·2	14·9	8·5	12·1	6·9	0
D 2	14·8	13·0	7·2	11·0	5·9	0
E 1	19·2	16·8	9·5	13·8	7·2	+++Xiphidiocercariae
E 2 (replacement)	19·0	16·5	11·0	13·0	6·5	+++*Fasciola*
E 3	23·0	20·5	12·7	17·2	9·9	0
Average A, B, C	18·7	16·3	9·8	13·5	7·5	
Average D, E	18·6	16·3	9·8	13·4	7·3	
Average D	16·0	13·9	7·9	11·6	6·4	
Average E	20·4	17·9	11·1	14·7	7·9	

L = length from apex to lower lip of aperture.
W = length of last whorl to lower lip of aperture.
B = breadth of last whorl in a plane parallel to aperture.
I = length of aperture.
b = breadth of aperture at widest part.

decreasing less rapidly than before and the curve tends to flatten out; such a flattening is almost certainly due to the snail becoming much less active as distress sets in. It is well known that active animals consume oxygen at a higher rate than do fasting, resting individuals. It should be remarked that in all cases (except when dying or dead) when the snails were returned to fresh water in the tubes, they resumed active feeding and crawling after a short time; when isolated again for the next experimental period they were to all intents quite normal once more.

(7) Fig. 4 shows that the hypothesis put forward previously to account for the anomalies in Table 4 is correct, though in this set of experiments the time period during which the differences in consumption are apparent is much shorter.

Two individuals placed together decrease the saturation value of oxygen in the water at a much photosynthesis of algae present on the shell, or the utilization of dissolved oxygen by algae, Protozoa and bacteria adherent to the shell if the experiment is carried out in dark conditions. The water used in these experiments was rendered as sterile as possible by boiling it before use, though bacteria may have been introduced in the re-aeration process by pouring necessary before use; though the shells were cleaned as thoroughly as possible before the snail was tested, by wiping, it is doubtful whether such wiping removes all the adherent organisms.

That oxygen loss from the water does, however, occur even with such precautions to a quite marked extent, probably because of bacteria or Protozoa and respiration by algae still adhering to the shell, is shown by the following experiments. For these, instead of enclosing living snails in the bottles, shells only were enclosed, these being from freshly collected snails similar to those used for the other

experiments. The animal was picked out of the shell, the inside of the shell wiped as clean as possible from living tissue and the outside of the shell cleaned in the same manner as for the experiments with living snails. Table 8 summarizes the results, using shells of approximately the same size as those used in the living animal experiments.

There is thus a quite measurable loss of dissolved oxygen with fresh shells only in experiments carried out in such shaded conditions, and this error should be allowed for in more critical work of the same nature. A slight loss is also recorded in the control blank over a 23 hr. period, but nothing like as great as that due to the shells. From the practical point of view, these experiments indicate that any method whereby the water in a natural habitat could be deoxygenated (and there are several such) would be likely to cause the death of at least the larger *Lymnaea*, the ones which are more likely to be infected; but conversely, *L. caillaudi* might in time show a dangerous adaptability to water of low saturation value, as its ability to decrease its oxygen consumption shows, if hard-pressed by control measures; but I have no evidence that such occurs under natural conditions.

Table 8. *Oxygen loss using empty shells of* Lymnaea caillaudi

No. of *Lymnaea* shells in bottle	Method	O_2 at start	Period of exp. (hr.)	O_2 at finish	O_2 loss	O_2 per hr. per shell
4	Under oil	7·1	3	6·4	0·7	0·06
4	Under oil	7·27	23	4·8	2·57	0·03
Control blank, 0	Under oil	7·27	23	7·2	0·07	—

Table 9. *Diurnal oxygen pulse, temperature, pH, and behaviour changes of* Lymnaea caillaudi *in a small fresh-water ditch*

Date	Time	Temp. °C.	*p*H	O_2 p.p.m.	% sat.	Snails	Weather
			Lower end of ditch				
28 Nov. 1944	0800	18·5	8·5	8·5	109	0	No sun
	1100	30·0	9·0	9·9	158	0	Sunny
	1400	35·5	9·5	11·4	204	+ Under water	Sunny
8 Dec. 1944	0800	18·0	8·0	9·0	113	+ + Under water	No sun
	1100	26·0	8·5	10·1	149	+ + Under water	Occ. sun
	1400	29·5	9·0	9·1	144	+ + Out of water	Occ. sun
	1630	28·0	8·5	8·5	130	+ + Out of water	Occ. sun
			Upper end of ditch				
28 Nov. 1944	0800	19·0	6·5	7·4	96	+ Out of water	No sun
	1100	32·0	7·0	12·3	212	+ Out of water	Sunny
	1400	36·0	7·5	11·1	202	+ + + Out of water	Sunny
8 Dec. 1944	0800	19·0	6·5	4·9	63·8	+ + + Under water	No sun
	1100	25·0	6·5	8·1	117	+ + + Out of water	Occ. sun
	1400	29·0	7·0	7·8	122	+ + + Out of water	Occ. sun
	1630	28·5	6·5	4·6	70·9	+ + + Out of water	Occ. sun

(Number of + indicates relative abundance at each time and place.)

(3) *Influence of dissolved oxygen on habitat selection*

A diurnal oxygen pulse is a common feature of most aquatic habitats (Welch, 1935), this being due to the photosynthetic production of oxygen by aquatic plants during the hours of daylight, and the utilization of dissolved oxygen by respiration of plants (and animals) during the hours of darkness. The abundance of algae in a suitable small habitat is such that during daylight a condition of oxygen supersaturation of the water is readily produced in spite of animal activity.

This occurs also under Kenya conditions, as the measurements given in Table 9 show. These were taken in a small clean-water ditch near Kabete, with a fairly large population of *L. caillaudi* and *Biomphalaria pfeifferi*.

This ditch had a depth of water of about 1 in. only, with a slight flow; the lower end was much more exposed to sunshine than the upper which had a fair growth of reeds. It is obvious from these results that a supersaturated condition of the water is quickly reached under these conditions after about 2 hr. daylight only, and that in spite of increasing water temperature, supersaturation values in excess of 200% may be reached during a sunny day; maximum supersaturation probably occurs sometime between noon and 1400 hr.

This was an interesting habitat, because by January 1945 after a long dry and hot spell, it was evident that considerable mortality was occurring among the snails in the ditch, which was formerly densely populated by both species. By this date

Biomphalaria had apparently completely disappeared from the ditch, and *Lymnaea* was very considerably reduced in numbers, only a few very small specimens being noted alive, and many dead and dying large ones being found. The mortality was most marked at the upper end of the ditch. No infection was found in the snails which would account for this mortality, but the ditch was observed to be very heavily overgrown with reeds now at the upper end, considerable amounts of organic trash having accumulated and a condition approaching stagnation produced (Pl. 7, photo 4). On 3 January at 0800 hr. the oxygen content of this semi-stagnant water was found to have a saturation value of only 37·2%, the lower end where there were more living snails having a saturation value of 85·5%. By 23 January at 0930 hr. only eight *Lymnaea* of medium size were found in this upper end after prolonged search, where formerly a few minutes' random collecting would yield 20–30; all *Biomphalaria* had disappeared apart from a few small specimens about 5 mm. long at the lower end of the ditch, where also a few small *Lymnaea* of similar size were found. Saturation values were 39·7 and 127% for the upper and lower ends respectively at this time.

These figures for oxygen tension at this depopulated upper end of the ditch are very similar to the distress values recorded in the laboratory experiments. Since no obvious chemical pollution or predators were present, the observations suggest that the depopulation may have been caused mainly by the deoxygenation of the water due to the choking plant growth and organic decay. Such deoxygenation would be even more marked at night-time, though an increase in oxygenation would be expected during the day. The preference of what few snails remained for the lower, more highly oxygenated end of the ditch is significant; and the death first of the larger snails confirms naturally what was found previously by laboratory experimentation.

In view of the probable importance of dissolved oxygen influencing the distribution of *L. caillaudi* in an area of available habitats, some observations have been made on a series of habitats round Kabete. These comprised 41 habitats of different types of which 11 were positive for *L. caillaudi*. Oxygen samples were taken at 0900 hr. for each series, all of them in sunny weather. By analogy with the diurnal pulse figures given above, the saturation percentage at this time had probably not yet reached its maximum value for the day.

The numbers examined were too small to construct a frequency table, but summarizing the results it was found that of 18 habitats examined whose saturation value was below 50%, only two were positive for *Lymnaea*, one of these being the ditch described above and the other a similar type of overgrown ditch where snails were more abundant; and of 23 habitats whose saturation value was 51% and over, nine were positive for *Lymnaea*.

The main features of these habitats are shown in Table 10, percentage saturation values being calculated on the temperature of the water sample at time of collection and corrected for an altitude of 6200 ft. While it is clear that the *Lymnaea* tend to occur only in those portions of the habitat areas having a high oxygen saturation value, some habitats with a high saturation value were negative for snails, other limiting factors such as intermittency and turbidity coming into play.

Of interest is the very low or absent dissolved oxygen in the stagnant swamps (habitat Q) or habitats with ferruginous waters.

(*e*) *Influence of temperature*

The normal temperatures found in natural habitats in Kenya appear to have little direct effect on *L. caillaudi*. I have found it living apparently quite happily in a shallow ditch whose water temperature was 36° C. at 1430 hr., and in the highland regions of Kenya Colony in some places it is capable of withstanding a diurnal variation of as much as 20° C. without obvious harm. The highest and lowest toleration limits have not been determined experimentally, but the snail is obviously able to accommodate itself to all the range of temperatures to be found in the cattle-rearing areas of East Africa.

During the short dry season in December to March when day temperatures tend to be maximal for the year, snails are in some habitats reduced in numbers, but it is probable that prolonged high temperatures exercise a detrimental effect in time through reduction of the oxygen tension of the water in which the snail lives; whether this ever happens without a concomitant effect of oxygen reduction, by excessive plant growth, at night-time and the process of organic decay, both of which are also accelerated by high temperature, is doubtful. The latter two factors are probably of more importance.

(*f*) *Influence of altitude*

L. caillaudi is capable of existing almost at sea-level (Mozley, 1939), and my highest altitudinal record is 7200 ft. in the highlands of Kenya Colony. There is no reason, provided other features of the habitats are suitable, why it should not occur higher than this, but I have had no opportunities of collecting in such areas. At heights over 10,000 ft. it is possible that the reduced oxygen tension at such altitudes may be a limiting factor, but this would tend to be offset by daylight photosynthesis producing supersaturation in a typical habitat. Such altitudes,

however, are not used as cattle-rearing areas in Kenya Colony.

(*g*) *Influence of sunlight and pollution*

Most *L. caillaudi* habitats are exposed to sunshine for most of the day and sunlight is probably a requisite of a good habitat; sunlight would have its chief effect in promoting a good growth of algae for food and oxygenation of the water, and as Boycott (1936) points out, such oxygenation also counteracts the pollution caused by decaying organic matter. Pollution by organic matter such as dead leaves, other trash and sawdust is inimical to *L. caillaudi*, and the snail is not found in habitats such as shaded forest pools floored with an accumulation of dead leaves, nor in forested streams (though here lack of light is probably the most important factor), nor in areas by sawmills where the water is polluted with sawdust (Mozley, 1944). Excessive fouling of the water by animal dung or camel urine, as in some waterholes in the Northern Frontier District of Kenya, is inimical, but slight fouling by dung in a running-water stock watering place is of no consequence to the snail, but of course of vital importance for the transmission of the disease. Where such watering places are closed ponds (habitats F or P) and the

Table 10. *Ecological conditions in waters positive and negative for* Lymnaea caillaudi

Series	Habitat type	Snails	Flow	% sat. O_2	*p*H	Inter-mittent	Weeds	Muddy	Shallow	Remarks
1	F	o	o	109	8·0	+	+	o	+	
	E	o	o	36	8·0	o	o	o	+	
	E	o	o	22·6	8·0	o	+	+	o	
	E	+++	+	65·0	7·5	o	++	o	+	
	E	+++	+	28·0	8·0	o	+++	o	+	
	E	+	+	72·8	7·5	o	o	o	+	
	D	o	o	65·4	8·0	+	++	o	+	
	D	+	o	56·5	7·5	o	++++	o	+	
	D	o	o	43·8	7·5	+	+++++	o	+	
	D	+	o	85·0	7·5	o	+++	o	+	
	L	+	+	101·0	8·0	o	+	+	o	
	L	o	+	67·5	8·0	o	+	+	+	
2	D	+	o	27·2	7·0	o	++++	o	+	
	D	++	+	90·9	8·0	o	++	o	+	
	K	o	o	16·8	6·0	o	+	+	o	
	D	o	o	27·5	5·5	o	+++	+	+	Iron bacteria++++
	K	o	o	28·0	6·0	o	++	+	o	
	D	o	+	82·1	6·0	o	+	o	+	
	D	o	+	81·9	7·0	o	+	o	+	Iron bacteria+
	Q	o	o	4·0	7·0	o	++++	+	+	Iron bacteria++++
	F	o	o	49·2	5·5	+	++	o	+	
	K	o	o	36·4	8·0	o	+++	o	+	
	K	o	o	63·9	8·0	o	+++	o	+	
	K	o	o	76·4	8·0	o	o	+	+	
3	Q	o	o	0·0	7·0	o	++++	+	+	Iron bacteria++
	H	o	+	55·7	6·0	o	+	o	+	
	D	++	+	106·8	8·0	o	++	o	+	
	D	+	+	102·1	8·0	o	+++	o	+	
	K	o	o	75·5	8·0	o	+	+	o	
	Q	o	o	51·5	7·5	o	++++	+	+	Iron bacteria++
	Q	o	o	2·1	6·5	o	++++	+	+	Iron bacteria++++
	Q	o	o	29·8	6·5	o	o	o	+	
	E	o	o	49·4	7·0	o	+++	o	+	
	Q	o	o	33·1	7·0	o	++++	+	+	Iron bacteria++
	Q	o	o	4·3	?	o	++++	+	+	Iron bacteria++++
	Q	o	o	0·0	6·5	o	++++	+	+	Iron bacteria++++
4	V	+	o	240·2	8·0	o	+	o	+	
	V	o	+	118·6	6·5	o	+	o	+	
	V	o	o	121·2	6·5	o	+++	o	o	
	V	o	o	96·3	6·5	o	o	o	o	
	V	o	o	200·1	6·0	o	++++	o	+	

(A plus indicates the presence of the condition, and in columns 3, 8 and 11, the relative abundance is indicated by the number of pluses.)

water has no opportunity of being constantly freshened by inflow, snails are absent. They are also absent in washing pools rendered soapy by constant use, though they may be present at the clear spring inflow of such a pool. A very good example of such was found in Central Kavirondo, where only the lower end of an elongated pool in a valley was used for clothes washing by the natives; at this lower end *Lymnaea* were absent, though they were exceedingly abundant at the top end of the pool where a clear spring trickle entered (Pl. 6, photo 2).

(*h*) *Influence of soil type* (*under water*)

The distributional survey of *L. caillaudi* in Kenya Colony is not sufficiently complete to enable any definite relation between the distribution of the snail and the geology of the area to be determined; nor has the soil distribution in Kenya been sufficiently studied as yet. Generally, however, the soils of the highlands and Lake Province area of Kenya fall into three main categories. These are red volcanic clay soils derived from decomposed volcanic tuffs (the red 'coffee' soils); the black 'cotton' soils derived from two sources—decomposed phonolites of Cretaceous age, and black soil which is formed upon gneiss and schist; and occasionally a type of gravelly clay which is probably derived from the weathering of granite, and related to the common 'Nyika' soils of lower altitudes (Gregory, 1921).

I have little data on soils from *Lymnaea* collections in the highlands, but for 37 collections of *L. caillaudi* from Central and North Kavirondo the distribution was as follows:

On black cotton soil (both types)	24 collections
On red soil	9 collections
On gravel	4 collections

It is probable that the nature of the bottom of a habitat is more important than the type of soil from which it is formed; a black cotton soil bottom in water forms a somewhat firm mud, on which the snails prefer to crawl. *L. caillaudi* is practically never found on a hard rock surface in water, or in streams where the bottom is composed of boulders, medium-sized shifting stones or coarse gravel, nor on a bottom composed of a loose flocculent mud or organic precipitate. In a small dam near Kabete, whose rocky bottom is covered by a loose, flocculent, sometimes deep deposit of green diatomaceous and desmidaceous 'mush' with little silt, *L. caillaudi* is very scanty although other conditions appear to be favourable.

The importance of a firm clay bottom for *L. truncatula* was first pointed out by Walton (1918) and Walton & Wright (1926), and Pilsbry & Bequaert (1927) stated that a mud bottom is a similar requirement of *L. natalensis undussumae*.

(*i*) *Influence of vegetation*

While *L. caillaudi* does not appear to be partial to any particular type of phanerogamic aquatic plants, algae on the bottom mud appear essential for their presence and also a certain amount of macrophytic vegetation, either emergent, like grasses or *Carex*, or floating, like *Potamogeton* and *Nymphaea*; the latter type of vegetation probably provides shelter and conserves the humidity near the water surface necessary for the snail's amphibious excursions. Where *Eischornia* or *Pistia* occurs in a suitable habitat, these snails are often found in the closely bunched axils of the leaves which usually hold a few drops of water, and they are often found crawling on the other macrophytic vegetation below water, feeding on the rich algal film encrusting the stems or on the underside of floating leaves.

The snails do not occur in channels which are completely bare of macrophytic vegetation but otherwise apparently suitable. Irrigated banana, sugar-cane and other vegetable *shambas* where the channels are kept constantly clean and cleared of all grass, etc., in the water are negative for *Lymnaea*. This was clearly illustrated at a channelled seepage in a vegetable *shamba* in Central Kavirondo, where two parallel channels, only a few feet apart and cut down from the same seepage head, were present; one channel had recently been completely cleared out by the owner and was entirely negative for *Lymnaea*, while the other had a moderate growth of rushes and abundant *Lymnaea*; both channels were in intercommunication by cross-channels (Pl. 7, photo 2).

On the other hand, where the water has such a dense growth of reeds and other plants as to cause stagnation and favour an iron bacteria growth, such water is also negative. This is the type of water found in habitat Q, which has already been mentioned in connexion with oxygen deficiency, and it may also evolve in a habitat previously favourable for snails as in the ditch at Kabete described above. Dense papyrus swamps are also of this nature. An area in Central Kavirondo again well illustrated this point, where two parallel seepage channels cut from the same seepage, one with a dense growth of rushes and scummy stagnant water, and the other with clear trickling water and few rushes, were respectively negative and positive for *L. caillaudi*, though within only a few feet of each other and intercommunicating (Pl. 7, photo 1).

Blockage of open-water channels by dense growth of the filamentous green algae such as *Spirogyra* also renders such habitats unfavourable for *Lymnaea caillaudi*.

Though *Lymnaea* may on occasion become carnivorous (Bequaert, 1928), their staple diet, as shown by intestinal examinations of numerous

freshly collected specimens, is vegetarian, consisting of microflora such as diatoms, chlorococcal algae and desmids which form a rich film on the bottom mud or encrusting plant stems in the water. They seldom, if ever, eat the tissue of higher plants, and small pieces occasionally found in their guts are probably accidentally rasped off by their radulae when scraping the microflora off plant stems and leaves in the water.

Good habitats invariably have a rich assortment of diatoms, desmids and other microscopic algae on the mud or plants. Table 11 shows the types available in different habitats round Kabete in January 1945, these habitats being chosen as both positive and negative for *L. caillaudi*. Identification of the algae is provisional only, since much remains yet to be done on the algae of East African fresh waters.

This table is compiled from only a few habitats in one locality at one time of the year and cannot be generalized upon, particularly in view of the fact that most fresh-water algae show a marked seasonal variation in numbers, being almost absent at some times of the year and very abundant at others.

Of the various genera of algae recorded, only Chlamydomonads, *Synedra* and *Navicula* are common to all the positive habitats at this time of the year, but they are found also in habitats negative for *Lymnaea*. There is probably no one type of algae necessary for the snails, and with which they are definitely associated; but there probably should be a sufficient abundance of chlorococcal forms such as *Scenedesmus* and diatoms such as *Navicula*. The quadripartite cells of the former and frustules of the latter are the commonest algae found in the intestines of the snails.

Habitats Q(1) and Q(2) listed in this table are two stagnant marshes with typical ferruginous and scummy water, almost completely deficient in dissolved oxygen (Table 10), and the poverty of the microflora and almost complete absence of the dependent microfauna is noteworthy. Obviously a snail would be hard put to it to find a square meal in such a habitat, apart from the risk of being suffocated while doing so!

Other limiting factors are probably involved in the absence of snails in the two negative portions of the dam and in habitats E and L, such as the lack of a suitable bottom, depth and turbidity of the water.

(*j*) *The biotic associations of* Lymnaea caillaudi *in Kenya Colony*

For organisms other than snails I have as yet little information owing to the paucity of ecological and systematic work on the common fresh-water invertebrates in East Africa. A species of *Nepa* is usually common in good *L. caillaudi* habitats, but I have never seen it preying upon this snail. A species of *Chaetogaster* is commonly found inside the shells of living *Lymnaea*, but it appears to be a harmless commensal. Information as to other predators such as fish is very scanty; the snails are usually absent in waters frequented by domestic ducks, which are noted snail-eaters (Cawston, 1937; Mozley, 1939, 1944).

The molluscan associations for *L. caillaudi* for 49 positive samples in Central and North Kavirondo and round Kabete district are as follows:

Occurring:

alone, 13 out of 49 samples.
with *Biomphalaria pfeifferi* (Krauss), 24 out of 49 samples.
with *Pila* Röding sp., 14 out of 49 samples.
with *Bulinus forskalii* (Ehrenberg), 7 out of 49 samples.
with *Biomphalaria sudanicus* (Bgt.), 4 out of 49 samples.
with *Succinea* Drap. sp., 4 out of 49 samples.
with *Bulinus tropicus* (Krauss), 2 out of 49 samples.
with *Physopsis globosus* (Morel.), 2 out of 49 samples.
with *Hippeutis* Charp. sp., 1 out of 49 samples.
with *Cleopatra* Trosch. sp., 1 out of 49 samples.
with *Melanoides* Oliv. sp., 1 out of 49 samples.

Occurring together in the same habitat with:

1 other species—18 samples.
2 other species—12 samples.
3 other species— 5 samples.
4 other species— 1 sample.

Unfortunately, the coefficient of association (Mozley, 1944) for these records cannot be calculated, as I have no records of the number of occurrences of these other species *without L. caillaudi*, a figure which is necessary for the calculation of the coefficient.

For Southern Rhodesian collections Mozley (1944) gives the following coefficients of association for *L.* '*natalensis*':

with *Biomphalaria pfeifferi*	1·59
with *Physopsis globosus*	1·31
with *Bulinus tropicus*	0·68

A coefficient distinctly greater than unity 'clearly indicates some other factor in the nature of physiological requirements or restrictions common to the two organisms' (Mozley, 1944).

The relationship between *Lymnaea caillaudi* and *Biomphalaria pfeifferi* in Kenya Colony is of some interest, because the two snails have a very similar habitat preference although *B. pfeifferi* may occasionally be found in water more polluted with organic trash than is suitable for *Lymnaea caillaudi*. The association is sufficiently close, however, to be taken with a fair measure of reliability as indicating the suitability of the habitat for the other species if only one is present, i.e. water with *Biomphalaria pfeifferi*

Table 11. *Microflora (provisional identifications) of habitats positive and negative for* Lymnaea caillaudi. *Kabete, January* 1945

Habitat type	D(1) Channelled seepage		D(2) Channelled seepage		V Dam			E	L	Q(1)	Q(2)
	Upper end	Lower end	Upper end	Lower end	Pool at side	Centre stream at head	Still water main dam	Shallow stream	Deep stream turbid	Stagnant marsh	Stagnant marsh
Snails (*Lymnaea*)	+++	+	+	++	+	o	o	o	o	o	o
Algae											
Volvocales: Chlamydomonads	+++	++	+++	++	+	+	+	+++	++	++	+
Asterococcus	++++	+	o	o	o	o	++++	o	o	o	o
Chlorococcales: *Chlorella*	++	o	o	o	o	o	o	+	o	o	o
Ankistrodesmus	+	+	o	o	o	o	o	o	o	o	o
Scenedesmus	+	+++	+	o	++++	++	++	o	o	o	o
Ulotrichales: *Ulothrix*	o	o	o	o	o	o	++++	+	o	o	o
Chaetophorales: *Chaetophora*	+++	+	o	o	o	++++	o	o	o	o	o
Conjugatae: *Spirogyra*	++	++	o	o	+	o	++	+++	+	o	o
Cosmarium	+	+++	+	+	o	o	++	+(2 sp.)	+	o	o
Sphaerozosma	+	+	o	o	o	o	o	+	o	o	o
Closterium	o	o	o	+	o	o	o	o	o	o	o
Bacillariales: *Synedra*	+	+	+++	+	+++	+++	++++	+++	++	o	o
Bacillaria	+	+	+	++	+	+	+	o	+	o	+
Gomphonema	o	o	+	+	+	o	o	o	+	o	o
Navicula	++	++	+	++ (2 sp.)	+	+	++	++++ (2 sp.)	++++ (sm. sp.) +(other sp.)	+ (2 sp.)	++
Pleurosigma	o	o	o	o	o	o	o	o	+	o	o
Tabellaria	o	o	o	o	++	++	o	o	o	o	o
Nitzschia	o	o	o	o	o	o	o	+	o	o	o
Gyrosigma	o	o	o	o	o	o	o	++	o	o	o
Euglenineae: *Euglena*	+	o	+	o	+	o	o	+	o	+	+
Cyanophyceae: *Merismopedia*	++	+	o	+	o	o	o	+++	+	o	o
Oscillatoria	o	o	++	o	o	o	o	o	o	o	+
Spirochaetes	o	+	o	o	o	o	o	+	o	o	o

+ = few present. ++ = fairly numerous. +++ = abundant. ++++ = very abundant.

only is often also a suitable habitat for *Lymnaea caillaudi*, a fact of some importance in surveying an area and planning control measures.

Since *Biomphalaria pfeifferi* is a highly efficient carrier of intestinal bilharzia in Kenya, the association should also convey its warning that to wade or bathe in water which apparently contains *Lymnaea caillaudi* only is not without risk, since infected *Biomphalaria pfeifferi* may also be present. Similarly when collecting *Lymnaea caillaudi* for fluke examination purposes, they should be collected with forceps, and if contact with the water cannot be avoided, this should be of the briefest possible nature, followed by thorough and immediate drying of the skin to minimize possible risk of bilharzia infection.

(*k*) *Behaviour of* Lymnaea caillaudi *in relation to its environment*

L. caillaudi is on occasions an amphibious organism, often being found a few inches out of water on the mud or herbage, and sometimes up to 30 ft. away from water (Porter, 1938), but I have never found it away from water in a dry place—even when out of water it is usually in contact with moisture on the mud, or in the dampness of emergent herbage. It is certainly not so 'terrestrial' as *L. truncatula* appears to be on occasions (Boycott, 1936), though it is probably unnatural for even the latter species to be found very far from permanent water (Peters, 1938), such instances as have been recorded probably being due to its mechanical transference by flood waters; probably neither it nor *L. caillaudi* can survive any length of time in the open, away from water. Such amphibious migrations must be of considerable importance in spreading *Fasciola* infection on herbage surrounding a habitat, since I have found *F. gigantica* cercariae to require very little water in which to swim and almost invariably they encyst on the nearest solid surface within a few minutes of being released from the snail.

Such data as have been collected on water temperature, relative humidity and oxygen tension of the water in relation to migration out of water is still somewhat scanty and rather confusing. Probably the relative humidity of the micro-habitat immediately surrounding the snail should be measured, rather than the general humidity near the habitat which has up to now been measured. Observations on a habitat at Kabete tend to show that *Lymnaea caillaudi* more often leaves the water when water temperature is reaching a maximum and is supersaturated with oxygen (viz. Table 9), and most often is found on exposed wet mud in hot noonday sunshine, which is an unexpected state of affairs. Such observations, however, require to be extended to cover 24-hourly periods.

The relation of the snails to cattle is interesting; they are seldom found in an area of water which is constantly disturbed by watering cattle, usually being present either upstream or downstream a short distance from the actual watering place. This is probably because of the mechanical disturbance of the water by the cattle, and perhaps also the intensive fouling of a small area by urine or dung.

Occasionally when conditions become unsuitable for some reason, *L. caillaudi* will leave the water in which it is living and will rather die of drought than return to the water. This is a very common feature in aquaria, and is one of the reasons why the snail is not easy to rear in captivity. This tendency is shown at all ages from newly hatched snails to large adults.

Occasionally also, when *L. caillaudi* colonizes new areas of flood water, it does not always seem capable of returning to a permanent habitat when the waters recede. A noticeable instance of this has occurred recently near Kabete where a small dam used for water supplies filled as a result of heavy rain and overflowed its steep rocky banks, the water filling numerous small potholes and larger pools on the previously dry slopes. *L. caillaudi* was found in great numbers in all these small pools, but when the dam waters receded again, the snails were stranded by hundreds in these pools and died when the water in them later dried up. Now the dam is practically free of *caillaudi* which at present is found only in small numbers by the inflow spring (Pl. 8, photos 1, 2).

6. GENERAL OPTIMUM HABITAT CONDITIONS AND CONCLUSIONS

While *L. caillaudi* may occasionally be found in habitats which are not primarily suited to it, it usually occurs in such habitats in very small numbers only. On the basis of the observations described in this paper it is possible, however, to formulate optimum conditions under which it may occur in large numbers. These would seem to be:

(1) Small size of water—small trickles are optimum, except in the case of *large* open-water dams, whose biological resemblance to running water has been noted.

(2) Stability of water—the water should not be subject to violent flooding (a feature linked to (1)), should not be seriously disturbed by cattle, and should be permanent in the dry season.

(3) Cleanliness of water—clear, clean water is optimum. Iron bacteria should be scanty or absent, as also suspended and colloidal silt and intense pollution.

(4) Openness of water—fairly open water not choked with vegetation is optimum; this is connected with the access of sufficient sunlight to

promote a good growth of food algae and adequate oxygenation.

(5) Shallowness of water—except in the case of large dams, deep water is inhibitive; 2–3 in. is an optimum depth.

(6) Current—a slight current, not strong enough to dislodge the snails, is optimum.

(7) Oxygen—the dissolved oxygen tension of the water is probably the principal factor limiting the distribution of the snail. It should be adequate at all times and probably not less than 75 % saturation at its lowest limit in a favourable habitat. The oxygen tension is, of course, related to all the above six factors.

(8) Hydrogen-ion concentration—a *p*H of 6·5–8·0 appears optimum.

(9) Total hardness—the water should contain sufficient calcium salts, probably not less than 10·0 p.p.m. measured as $CaCO_3$.

(10) Presence of a mud bottom—a mud bottom, not too flocculent and preferably a black clay, is optimum.

(11) Plants—the presence of a *small* amount of water weeds, and an abundance of algae of diatomaceous and chlorococcal nature is optimum.

(12) Predators should be absent.

(13) Temperature and altitude are probably not in themselves important in Kenya, but may have an indirect effect through oxygen tension of the water.

There are probably other factors necessary in an optimum habitat which have not been studied. For example, the absence of chloride and copper ions is probably necessary, since both are toxic to the Lymnaeidae in very high dilutions. In general, however, the factors outlined above are those which can be readily assessed without elaborate sampling and measurement, except oxygen; but good habitats having a high oxygen saturation value are usually recognizable as such.

In all, *L. caillaudi* is thus very similar in habitats to the Palaearctic fluke vector snail *L. truncatula*, the best definition of whose habitat preferences is given by Peters (1938). Generally, these preferences are also very similar to those described for the Schistosome carrier *Biomphalaria pfeifferi* in Sierra Leone by Gordon *et al.* (1934), though the domestic tendencies of *B. pfeifferi* are more evident in this part of West Africa; and they are not unlike the habitat conditions preferred by the schistosome vectors *Planorbis boissyi* and *Bulinus contortus* in Egypt (Barlow, 1937).

Table 1 summarizes the chief types of habitats to be suspect as 'fluky' areas, and on which attention should be concentrated for control purposes. In series 1, most or all of the above factors are favourable, in series 2 one or more are usually absent, and in series 3, most or all are unfavourable.

As Boycott (1936) has pertinently remarked, the final effect of ecological factors is their sum; the beneficent effect of some may be overridden by the unfavourable effect of others, and in any one habitat one or more factors may be limiting in nature. Only in a very good habitat are all the conditions favourable all the time; seasonal changes may play some part in controlling the abundance and distribution of the snail.

7. SUMMARY

1. *Lymnaea caillaudi* Bgt. is the principal and most efficient vector of fascioliasis in East Africa.

2. This species of snail occurs very widely in the Ethiopian region, regardless of watersheds, from Egypt to South Africa, and Sierra Leone to the east coast.

3. The various types of aquatic habitats available in East Africa are described, and the snail occurs mainly in those habitats found at the heads of valleys.

4. The habitats in Tanganyika and Southern Rhodesia favoured by the snail are generally similar to those in Kenya, but in the Belgian Congo it occurs chiefly in temporary collections of water.

5. The hydrogen-ion concentration of the water has little effect on the distribution of the snail, but the optimum range is *p*H 6·5–8·0.

6. The total hardness of the water has little effect on the distribution of the snail, but the lower toleration limit is probably about 8 p.p.m. $CaCO_3$.

7. In Kenya Colony, the water in a good habitat is usually clear, clean, permanent, shallow and with a slight current. Ferruginous waters are unfavourable.

8. The oxygen tension of the water is probably the chief limiting factor and should preferably not fall below 75 % saturation. The snails die of suffocation below 10 % saturation, but show distress below 75–85 % saturation. In closed containers the oxygen consumption is not constant, but after an initial rise shows a sharp decrease to the distress saturation value of the dissolved oxygen and thereafter a more gradual decrease till death supervenes. The relationship between decrease of saturation and decrease of consumption is not proportional. Even under natural conditions, the snail is probably not independent of either moisture or dissolved oxygen in the water.

9. Sunlight and lack of intensive organic pollution are essential in a good habitat.

10. Normal temperatures and altitude have little influence on the distribution of the snail.

11. While the snail is more prevalent on black cotton soils, the nature of the bottom is more important, and this should be a firm mud, not flocculent. Rocky bottoms are seldom favourable.

12. While the snail is not associated with any definite species of plants, a good habitat is characterized by a certain amount (not too much) of macrophytic vegetation and a sufficient abundance of diatomaceous and chlorococcal algae for food.

13. Predators should be absent in a good habitat. *L. caillaudi* shows a marked association with *Biomphalaria pfeifferi*, a carrier of intestinal schistosomiasis, both in Southern Rhodesia and Kenya Colony.

14. *Lymnaea caillaudi* is at times an amphibious snail, but is not found away from moisture even when out of water. The factors controlling such amphibious excursions have not been clearly determined, but the snail will sometimes not return to the water which it has left.

15. A general résumé of conditions in a favourable habitat is given, together with a list of habitat preferences (Table 1).

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WATCHING NOCTURNAL ANIMALS BY INFRA-RED RADIATION

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(With Plates 9 and 10)

1. INTRODUCTION

The detailed study of the behaviour and habits of wild nocturnal vertebrates presents many difficulties. It is almost impossible to make continuous observations by watching at the time when the animals are most active. Apart from mechanical recordings of regular activities, information must largely be based on deductions drawn from cries made by the animals in the dark, and from occasional glimpses obtained with a light which usually disturbs the creature being watched. Crawford (1933) and Park (1938), in the tropical rain forest of Central America, studied the periods of activity of various species at night by noting their calls; Crawford also used a torch with which he could pick up the eye reflexion and often identify the species.

Flashlight photography has been developed to a very high standard, in this country by Hosking & Newberry (1945), and in the United States by Gregory (1940). Hosking & Newberry particularly mention the difficulty of determining from a hide at night what the animals were doing, but Gregory found it possible to use a light to watch his subjects. Flashlight photography has the disadvantages of often depending on the animal to release the flash mechanism, which it may do when not in a suitable position, and of merely recording a very small incident—often trivial—in a whole night's activity.

Some nocturnal animals prolong their activities from dusk to dawn so that there is sometimes a short period with enough light for watching. Rabbits (*Oryctolagus cuniculus*) are one of the few animals which have been watched in this way (Southern, 1940).

Chitty & Shorten (1946) conditioned wild rats (*Rattus norvegicus*) to feed under artificial light in order to watch their behaviour. The observations so made were, however, open to the objection that the rats' behaviour might be different under artificial light from what it is in the dark.

A new method using infra-red radiation seems to overcome many of the difficulties of night-time studies and has been successfully tried out on a colony of wild rats (*Rattus norvegicus*) near Oxford.

2. DESCRIPTION OF THE APPARATUS

The apparatus used for viewing rats by infra-red light consists of an infra-red transmitter and an infra-red sensitive telescope about 1 ft. in length and 2½ in. in diameter (German 'Vampir' pattern). The transmitter consists of a 6V. 24 W. tungsten filament lamp mounted in a car headlamp, and screened with an infra-red filter*. The reflected infra-red light is focused by the objective lens of the infra-red telescope on to the photosensitive cathode of an image converter tube, the electron pattern so released being accelerated towards the anode where it strikes a fluorescent screen and produces a visible picture in green which is viewed through a 1·5 × magnifying eyepiece. The potential difference between the anode and the cathode of the image converter tube is maintained at 11 Kv., which is obtained from a transformer unit (in a cylindrical case 10 in. long by 5 in. in diameter) working from a 6 V. car battery. Since the transformer unit made a continuous high-pitched hum, it was fitted with long high-tension leads, so that it could be carried away from the area in which observations were being made. This precaution was probably unnecessary with rats, since on the few occasions when the transformer unit was left in the shed they took no notice of it.

The lamp and telescope were mounted and aligned as one unit, the lamp focus being adjusted to provide a bright central spot together with a lower level of general illumination over the whole field of view. The lens of the telescope allowed of focusing on objects down to about 4 ft. away, but working at this distance would have been less satisfactory, since focusing was by means of an ordinary pitch thread, and this could not be moved back and forward sufficiently quickly to keep moving objects in view. The depth of focus of the image is approximately the same as with a camera, so that it was found best to work at a range of about

* This filter was known to transmit radiation between about 19,000 and 6000 Å, but full spectral transmission was not measured. The human eye is sensitive to wavelengths ranging approximately from 7000 to 4000 Å.

9 ft., and to concentrate the rats' activities at this distance by means of bait. The detail of the image is not so critical as that produced directly through a camera lens, but is quite good enough for observing movements and behaviour, and for identifying individual rats by peculiarities of their appearance.

In addition to this apparatus it was necessary to have an auxiliary light source for taking the photographs. A floodlight was considered more satisfactory than a flashlight, since there was no troublesome changing of flashbulbs involved every time that an exposure had been made. Furthermore, the use of a focused flood light concentrated attention on the central object of the picture without bringing in disturbing detail of the surroundings. The lamp used was a large headlamp, using a 200 W. bulb silvered at its further end, so that all the light was directed back towards the reflector and an even pool of illumination thrown. This headlamp was run off a 12 V. car battery, and was wired up with a push-button switch, so that it could be turned on at the instant it was desired to take a photograph and turned off again at once. In this way too hasty running down of the battery was avoided. This floodlight, just like the headlamp mounted on the telescope, had an infra-red filter fitted over the glass.

To adjust the beam of the floodlight it was only necessary to switch on the telescope, and the best arrangement could be reached by trial and error. During the first few days of photographing the floodlight was sited so that it pointed down on to the ground at an angle of about 30°, and it and the camera were placed one on either side of the telescope. Camera lens and flood thus converged on the object at an angle to each other of about 45°. This arrangement was not very satisfactory, since the beam striking the floor created a pool of light, whose long axis lay slantwise across the field of view of the camera. Since all our set-up was designed so that the rats should move into view along the belt of focus of the camera and not across it, the position of the flood was changed to elongate its beam at right angles to the axis of the camera lens. This arrangement had the disadvantage of throwing rather long shadows from the outlines of the rats, but the only alternative of having the source of the flood almost vertically above the rats could not be managed.

Once this was all set up the outline of the floodlight beam was marked out on the floor with pebbles at the direction of somebody looking through the telescope, and then outlined with chalk. This meant that, while normal observations were going on, this area in the middle of the field of view was readily distinguishable on the screen of the telescope and the optimum position of the rats for photographing could be judged nicely. A further extension of this principle was to draw a chalk line at right angles to the camera axis showing exactly when rats were in the belt of sharpest focus.

The actual technique of the photography had no complications. The camera was set up alongside the telescope, focused first of all on a torch face, and the lens then set forward 1/250th of its focal length (8½ in.), to make allowance for the different position of focus of the infra-red rays. The plates used were Kodak Infra-red Extra Rapid, the lens was used throughout at full aperture (f 4·5) and the exposure varied from 1/20th to 1/50th of a second, since a Luc silent shutter was used which gives variable exposure according to the amount of pressure exerted on the release. The whole procedure was easily done by one person seated at the telescope and watching the whole time exactly what happened; one hand rested on the push-button for the flood and the other on the camera release. Many exposures were spoiled by movement of the rats, but with the available apparatus it was not possible to take them at a faster speed or to increase the power of the flood or the aperture of the lens.

The advantages of this method of taking photographs in the dark are sufficiently startling not to need stressing. Any animal that can be drawn to a prearranged spot by baiting or other means of attraction can be photographed in this way under continual observation to determine the right moment to take the pictures.

3. SENSES OF ANIMALS IN RELATION TO INFRA-RED RADIATION

The apparatus described herewith has certain limitations in its application to observing and photographing nocturnal animals. First of all we may briefly consider whether the animals will be entirely unconscious of the illumination to which they are being subjected.

There is a considerable amount of literature on the sensitivity of the vertebrate eye to light of different wave-lengths; only a preliminary search has so far been carried out. As far as mammals are concerned, rabbits and mice are apparently stimulated little by red light but more by the higher wave-lengths from orange upwards (cited by Parsons, 1924). Walton and Bornemayer (1938) claim to have shown that the white rat is rather sensitive to red light but most other workers on this subject, as Walls (1942) points out, are generally agreed that rats and other nocturnal rodents have a reduced sensitivity to the red end of the spectrum. Hess (1915) compared the pupillomotor reaction in man, pigeon, long-eared owl (*Asio otus*) and rabbit, and found that the nocturnal bird and mammal both reacted far less to red than man or pigeon, but far

more to blue, the maximum reaction being to blue-green. From a number of papers on birds (e.g. Abelsdorff, 1907; Meyknecht, 1941) it is clear that there is a distinction between diurnal and nocturnal forms, in that the latter respond more readily to medium wave-lengths, such as blue-green and blue, while diurnal birds find their maximum in the orange band. Meyknecht, working with the little owl (*Athene noctua*), found that it had no difficulty in discriminating between yellow, green and blue and corresponding shades of grey, but that the distinction between red and grey was very difficult. This, of course, is a species which is far more diurnal than other British owls. Hess found in the case of the long-eared owl (*Asio otus*) that the pupil reaction to blue-green and blue light was very sensitive, and this is supported by the previous work of Abelsdorff.

All the available evidence therefore suggests that the eyes of nocturnal animals, far from being sensitive to infra-red, are hardly sensitive to visible red. Mention must be made here of the rather surprising results of work by Vanderplank (1934), who investigated the reactions of a tawny owl (*Strix aluco*) and gave facts which appeared to show that their eyes were sensitive to infra-red, and that they were able to locate and catch prey at night by the aid of long-wave radiation from the earth and from the prey themselves. Matthews & Matthews (1939) tested this hypothesis on the same species and were unable to show any positive reaction of the tawny owl's eye to infra-red light. Since this the work by Dice (1945) has shown beyond reasonable doubt that owls are able to catch their prey in apparent darkness by reason of the extreme sensitivity of the coneless retina to blue-green and blue light and of the wide 'aperture' of the eye. Infra-red illumination was of no use to the species tested in aiding them to find prey, but in visible light of as low an intensity as 0·000,000,73 f.c., they could find them at a distance of 6 ft.

Nevertheless during this work it was commonly noted that rats would bolt when the floodlight was turned on. This reaction varied and was most commonly elicited when the rats were nervous for some other reason or were just emerging from cover. Some individuals hardly ever took the slightest notice of the floodlight, while others would apparently disregard it if several rats were setting them an example.

But the fact that at times they appeared conscious of something is important when the limitations of the method are being considered. There seem to be two possible explanations. Both the floodlight and the headlamp mounted on the telescope emitted a small amount of visible light; inspection in the dark revealed a faint and very deep red glow, so it is possible that this was apparent to the rats. However, it is more probable that they could perceive the immediate rise in temperature caused by the floodlight beam. This is supported by the fact that the headlamp, giving out far less heat, was entirely disregarded by the rats.

The problem needs further work, but it is worth mentioning another fact of some interest. Under certain circumstances the eyes of rats reflect the infra-red rays back into the telescope with considerable efficiency. The capacity of the vertebrate eye to reflect back visible light is well known in nocturnal animals, and one worker has used this phenomenon for studying the habits and movements of nocturnal birds (van Rossem, 1927). Later information given by Marshall (1939) amplifies this: the eyes of *Otus flammeolus* reflect in this way at a distance but not at close range, presumably because of the contraction of the pupil under the stronger stimulation. Thus the fact that the eyes of rats give back this remarkable glow at close range suggests that the infra-red rays do not stimulate the pupil to contract. However, further observations are needed on this point, which is yet far from clear, since the power of reflection depends also on the individual rat (Pl. 10, photo 5).

At the moment the situation is as follows: with the telescope and its accompanying headlight, there seems no evidence at all that brown rats are capable of detecting the rays. Observations on habits and location of other nocturnal mammals and birds is therefore likely to be feasible by this method. Under the more intense illumination of the floodlight results are not quite so easy, though this may merely be due to the heat which so powerful a lamp emits.

4. LIMITATIONS OF THE APPARATUS FOR NIGHT WORK

The efficiency of the telescope is entirely dependent on the strength of the illumination provided. With a powerful enough searchlight it will give a satisfactory image of a distant scene, though of course fine detail becomes progressively more difficult to make out.

Needless to say, expense and difficulties of transport will increase if the power of the light source is increased greatly, and a point is soon reached at which a portable battery can no longer be used.

The present Vampir apparatus could be adapted quite well for carrying about in the field, though for any continuous observation a stand upon which to mount it would always be necessary. The life of a battery made to carry on the back would be fairly short, if the headlamp was used frequently, but with arrangements for continual servicing, this would not be an insuperable difficulty.

Photo 1.

Photo 2.

Photo 3.

Photo 4.

Photo 5.

5. WATCHING BROWN RATS

In the course of war-time rodent control research under the Agricultural Research Council experiments were made at a pig farm where a shed was reserved for baiting rats. A grid of 9 in. squares marked in a concrete floor (see illustrations) was useful for plotting positions. These rats were entirely wild and at the time of the present observations (August 1946) obtained most of their food by scavenging. Previous populations had been observed at night after a short period of conditioning to artificial light (Chitty & Shorten, 1946). When wheat was given many rats carried it away under cover and the time actually spent collecting the grains was only a few seconds at each visit. Other individuals remained eating for various lengths of time without running to cover.

Observations were made on the way in which rats behaved after a change had been made in their environment, for the remarkable sensitivity of this species to unfamiliar situations is an important factor in rat control. Thus the introduction of a piece of wood or a bait container stopped the rats from feeding.

Similar observations were made with the infra-red apparatus and it was satisfactory to find that the behaviour of the rats in the dark was much the same as that seen in other individuals by ordinary light. The habit of carrying wheat under cover was strongly marked in a proportion of the rats, so that there was constant traffic to and from the bait. When feeding on flour, rats spent a longer time in view (Pl. 9, photo 2) but still ran frequently to cover. Individual characteristics were very obvious: one rat in particular seldom carried its wheat away (Pl. 9, photo 1) while another was noticeable for its extreme nervousness even under familiar conditions.

At the beginning of each night's watch a handful of bait was placed on the floor and feeding usually became well established within a few minutes. After this the effect of placing a 'new object' was studied and again there were great individual differences in reaction. When bait was placed in a tin lid most animals approached within a few inches before becoming conscious of the change. Some cautiously examined the lid (Pl. 10, photo 3) and then stayed in its vicinity picking up the few grains left on the floor. Others, after their first discovery, drew back violently, skirted the new object at a distance of 2–3 ft., or left the shed entirely. The nervous movements of the majority of rats and their subsequent retreat from the area made it difficult to photograph typical reactions. Sometimes the rats took comparatively little notice of objects such as a small glass bottle, placed a few inches from the food (Pl. 10, photo 4). In fact the chief difference in behaviour from that seen under ordinary light seemed to be that objects were not appreciated from as far away.

Thus for most purposes artificial light is satisfactory for watching the brown rat at night. However, this species is not as strictly nocturnal as many others, e.g. Blair (1943) has shown that the deer mouse (*Peromyscus maniculatus*) is inactive even in very dim light. For such species observation with the infra-red apparatus has tremendous possibilities.

6. SUMMARY

1. Most nocturnal vertebrates cannot be watched during the greater part of their normal activities and successful photographs are often a matter of chance.

2. By means of infra-red radiation and a special telescope it is now possible to make continuous observations on nocturnal species which generally have poor sensitivity to light of the longer wave-lengths.

3. This technique has been successfully used to study and photograph the brown rat (*Rattus norvegicus*).

7. ACKNOWLEDGEMENTS

We wish to acknowledge our great indebtedness to the Ministry of Supply and especially to the Superintendent of the Army Operational Research Group for making available to us the apparatus with which this work was done. Members of his staff also very kindly gave us their time for working out an adaptation of the apparatus suitable to the particular circumstances. Acknowledgement is also made of the help received from Mr D. Kempson in processing the photographs.

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* Original paper not seen; quoted from Bailey & Riley (1931).

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REVIEWS

AMERICAN FISHERIES

[I. N. Gabrielson] (1945). *Fishery resources of the United States. Letter of the Secretary of the Interior transmitting pursuant to law, a report on a survey of the fishery resources of the United States and its possessions.* 135 pp.; numerous text-figures. U.S. Government Printing Office, Washington. Price 40 cents.

This document 'is planned primarily for the Congress, at its request, with the idea of giving to busy people, in condensed fashion, a perspective on its subject'. This aim is brilliantly achieved. A typical page gives a drawing of the animal, its distribution, a sketch of the commercial gear employed and a text account usually of 100–1200 words. Well over 150 species of fish are dealt with, together with whales, fur seals, shellfish (oysters get six pages), Crustacea, sponges and a few other marine and fresh-water animals.

The amount of space given to each species or group is determined chiefly by its economic importance, which is obviously the best way of attracting a legislator's attention. Thus we learn that the total capitalized value of U.S. fishery resources is almost $6,000,000,000, that 500,000 tons of pilchards are caught annually on the Pacific coast, that 5000 fishermen are normally engaged in the Great Lakes industry, and that even edible frogs are worth a million dollars a year.

Since the economic aspect of these resources is the keynote, biological information is chiefly limited to that with the most obvious bearing on management. This is natural in a book of its nature, since the passage of important laws does not call for details about growth zones of fish scales or bilateral cataracts in trout. On the other hand, it is important for congressmen to know that whitefish (*Coregonus clupeaformis*) do not mature below a weight of 2 lb., that weakfish (*Cynoscion regalis*) migrate from New York to Virginia in their first summer, and that tunas are no respecters of territorial waters. These biological facts should set the pattern for concerted action upon legal limits and intensity of fishing; but unfortunately the level of regulation is all too often set by the least enlightened of several states or countries which share the same resource. Since the management of its fish and wildlife is the jealously guarded right of each state, the lot of a federal agency is not a happy one, though there are many problems which can best be tackled on a national scale. Haddock, for example, though primarily a resource of Massachusetts, is sold all over the U.S.A., and the best utilization of the stocks is obviously an interest of the whole country. At the technical level there is also a lamentable failure to adopt the best procedure, for example, in stream improvement and the design of fish ladders and screens on irrigation ditches. Those who are only acquainted with problems of European politics are in no position to understand the complexities of the Federal-State and Dominion-Provincial relationships of North America.

Throughout the book are damning examples of over-exploitation: whaling, once the most important marine resource, employed only three boats and 59 people in 1943; the annual catch of Great Lakes ciscoes (*Leucichthys artedi*) has dropped from a peak of 39 million pounds to less than a million, and the greater part of about 1600 sq. miles of public oyster reefs have been depleted. There are all too few examples of what can be done by proper management. The catch of herrings in Alaska is controlled by allotting an annual tonnage quota determined from up-to-date knowledge of brood strengths (Canada has a similar system and three states adopt other methods); but the only really well-run industry is the Pacific halibut fishery. The International Fishery Commission was established in 1924 to study the halibut and was later given regulatory powers as a result of which the annual yield is now 10 million pounds greater than it was in the days of unrestricted fishing. The fur seal is another example of what can be done to restore a depleted resource, though the next stage—its best utilization—has yet to be worked out. Since 1910 the Alaska herd has increased about tenfold and now numbers almost three million.

It will be realized from the examples already given that an immense amount of valuable information is contained in this document, available at the absurdly low price of 40 cents, and there is probably no other single source of such wide information on the U.S. fisheries. It is therefore a pity that no references are given to the publications from which the facts are drawn, though it is perhaps unfair to criticize a work for failing to do what was not intended. Although a price list of the regular publications of the Fish and Wildlife Service will be sent on request, it would have increased the value of the work if the key papers, at least, had been given. This could have been done without overburdening busy congressmen and it might, indeed, have been instructive for them to learn the vast amount of research and organization underlying the facts so simply placed before them. To take a species at random: the information on striped bass (*Roccus saxatilis*), which occupies 1¼ columns, is mainly based on a 77-page paper covering over two years' work involving specialized studies of spawning habits, growth rates, age at maturity, migrations and food habits that was financed (in the conglomerate fashion typical of much ecological work) by a group of Connecticut sportsmen, the Connecticut State Board of Fisheries and Game, the American Wildlife Institute, the U.S. Bureau of Fisheries and the North Carolina State Department of Conservation and Development (Merriman, D. (1941). Fishery Bull. U.S. Fish. Wildlife Service, 50, No. 35: 1–77). This is not to say that the book fails to stress either the lack or importance of basic research; indeed the following type of phrase recurs with great frequency: 'Little is known about the biology of white sea-bass', 'little is known about marlins', 'knowledge of [our Atlantic herring] is meagre', 'conservation of the lake trout will require extensive investigations of its biology'. It remains to be seen how much ice this will cut with

Congress, but there can be no question of the urgent need for more scientific work and for the much harder task of getting legislative action on the basis of what is already known.

Rather more could have been done to bring out the general principles of fishery management, though the grosser abuses such as pollution, erosion and river obstruction are briefly dealt with, as well as the increasingly doubtful value of hatcheries in restoration programmes. Plenty of material for such a discussion is already in the book, but it is scattered under geographical and species headings and not altogether easy to extract. Alternatively the index could have been more complete. Although we find 'By-products, value of' we do not find 'Management, examples of', and it is equally impossible to track down several fascinating pieces of information only partly digested in a first reading. Thus I am still looking for the account of a fish which was at one time sold for fertilizer at (I think) one dollar a wagon-load. Similarly it took some time to rediscover what fish (or mollusc or crustacean?) 'belongs' chiefly to one state but is widely sold throughout the U.S. (*Answer*: Haddock to Massachusetts).

These remarks should not be taken as a reflexion upon the remarkable skill with which the anonymous authors have presented so much material. On the contrary, the extreme interest they arouse in a large and difficult subject compels the reader to refer continually to their examples.

DENNIS CHITTY

QUATERNARY CHANGES

F. E. Zeuner (1945). *The Pleistocene Period, its climate, chronology and faunal succession.* Vol. 130, x + 322 pp., 76 figs. The Ray Society. Price £2. 2*s*.

F. E. Zeuner (1946). *Dating the past. An introduction to geochronology.* viii + 444 pp., 24 pls., 103 figs. Methuen and Co., 36 Essex Street, London, W.C. 2. Price £1. 10*s*.

Problems of historical biogeography dealing with the evolution of floras and faunas are often approached with scant reference to the evolution of the environment. When transoceanic land bridges are postulated, or whole continents are made to drift in order to support some distributional theories, little attention is usually paid to the climatic conditions which may make the best bridge unusable for a certain plant or animal. Plant geographers are, in this respect, well ahead of zoologists, and H. Godwin's studies in the post-glacial history of British vegetation may be quoted as an outstanding attempt to analyse the present-day plant associations in relation to their environment on the basis of the evolution of that environment during the Quaternary period. Attempts of a similar kind have been made also by students of faunas, but such attempts are often remarkable by their boldness rather than by the weight of supporting evidence. One of the reasons for this is not so much the lack of reliable information on the geological evolution of lands and their climates, as the fact that such information is not easily accessible to biologists, many of whom are blissfully ignorant of its existence. The two books under review should go a long way towards helping a zoogeographer to analyse a fauna from the point of view of dynamic ecology.

The first book, on the climate, chronology and faunal succession in the Pleistocene period, contains abundant and well-arranged information on the climatic fluctuations during the Pleistocene mainly in Europe, but with some, necessarily less complete, data on other regions. The last chapter, dealing with the faunal evolution in the Pleistocene, will be of special value for students of the history of European fauna.

The second book provides, in the first two parts, an instructive introduction to the methods used in studying the post-glacial climatic fluctuations; tree-rings, varves and pollen analysis. The third part deals with the phases of the Ice Age and with the pluvial phases of the warmer countries. The concluding chapter of the fourth part deals with the biological evolution and time, a problem that should be of considerable interest to ecologists.

It is only natural that a science dealing largely with reconstructed evidence and without possibility of experimental approach is subject to grave limitations, and a high proportion of deductions and conclusions have to rest on a slender foundation of facts, reinforced by more or less probable hypotheses. It would be easy to dismiss such reconstructions of past environments and populations as purely speculative; but it might be useful to remember that even the most matter-of-fact ecologist enters the field of speculation as soon as he attempts to analyse his subject. The only way to avoid speculation is to restrict one's activities to purely descriptive work and to avoid developing any theories, but this is hardly the way to progress.

Dr Zeuner's books may encourage speculation in those who are inclined to speculate in any case, but the author is careful in pointing out the need for a critical evaluation of all evidence, and purely hypothetical conclusions are presented as such. The biogeographers who wish to consider their data in the light of data from allied sciences will welcome the abundant and well-classified bibliographies.

B. P. UVAROV

A FAUNAL MONOGRAPH

E. B. Ford (1945). *Butterflies.* The New Naturalist Series. xiv + 368 pp. 48 colour plates (including 56 colour photographs of living specimens by S. Beaufoy), 24 black and white plates, 32 distribution maps and 9 other diagrams. Collins, 14 St James's Place, London, S.W. 1. Price 16*s*.

It is difficult to review this book satisfactorily; it has the high quality that merits vigorous criticism, and to do full justice to its wide scope would need a long essay. Dr Ford has set himself a task which has not, so far as I know, been previously attempted. He surveys, and for the most part with admirable lucidity, many of the major problems of modern biology in terms of what is known, or can be inferred, about the 68 British species of butterflies. He has thereby imposed upon himself severe limitations which on a few occasions, however, he has been forced to abandon. In the result, he has produced a most valuable compilation of our knowledge about this small group of species—the more valuable because he has specifically drawn attention to the gaps in that knowledge. But in restricting himself where possible to examples drawn

from butterflies he has not always made it easy for the inexpert reader to grasp the framework of the problems illustrated. If he has failed in this, at any rate he has failed gallantly.

Dr Ford opens with a delightful short sketch of butterfly collecting in this country during the last three hundred years and passes on to deal with structure, senses, classification, habits, distribution, means of dispersal, and genetics, adjusted, in his own words, 'to converge upon the last three chapters which are all concerned, directly or indirectly, with evolution'—the subject which he rightly regards as the 'key-note of biological study and research'. As might be expected, Dr Ford is perhaps happiest in dealing with genetics, though it is here that he is often cramped for lack of direct examples from work on butterflies. By going further afield he might have emphasized more clearly the work which still needs to be done, and which for the most part can be done by keen amateurs. It would be difficult, however, to carry out some of the experiments suggested without greater facilities than are normally available to the non-professional entomologist. Again, in spite of his clear definitions of technical terms, the treatment of structure is heavy going for anyone without some morphological training; but the reader must not allow this formidable obstacle to deter him from reaching the fertile fields beyond, and his way is lightened by many happy touches such as the comment on the tastes of the purple emperor on p. 95.

Since evolution is the central theme, it is all the more surprising that ecological problems are hardly touched on; and the reader can only infer that the field for ecological work in this group is wide open. If this is indeed true, one would have expected Dr Ford to pay particular attention to a subject so eminently suitable for further study by field naturalists. But he disclaims, for instance (p. 90), any intention of giving lists of larval food-plants on the grounds that these facts can be obtained from other sources; so can other sets of facts which he has nevertheless included and upon which by so doing he has shed new light. In Chapter 7 he endeavours to treat geographical and ecological distributions as a single subject and thereby tends to obscure the salient problems of each as well as the true extent of their interconnexion. In dealing with the vexed problem of adaptation, as opposed to adaptability, he not infrequently makes assertions which at the best are no more than guesses, and guesses of a controversial kind, without making it clear that these questions must be regarded as still *sub judice*. In this he departs from the high critical standard he clearly displays in dealing with inferences within the genetical field. But even if these defects are given their maximum weight, the book still remains one from the study of which the field ecologist can draw much knowledge essential to his work. He can find here collected and clearly set out many facts of which he must take careful note; but he would be well advised to put aside for the present some of the more theoretical interpretations, and to proceed with an open mind to acquire a greater insight into the complex structure of natural populations and of their relations with the intricate and variable network of their environment before he returns to the fascinating game of theoretical synthesis. In the present state of our ignorance it would be as rash to assert that Dr Ford's interpretations were wrong, a sir would be unwise to allow them to over-colour out advancing thought.

The absence of sufficient ecological data and of more detailed indications of distribution outside these islands, more particularly in regard to northern limits, makes it difficult to assess the true value of some of the arguments adduced in Chapter 14. But the 32 maps of the British distributions are a welcome addition, and it is to be hoped that they will stimulate the eventual carrying out of a proper distributional census comparable to that which has long been maintained for land and fresh-water Mollusca (it is curious that the editors seem unaware (p. xiv) of this excellent work).

The photographs in general are admirable, and Dr Ford is to be congratulated both on including views of typical and celebrated habitats and on the wealth of material he has managed to reproduce in his plates of set specimens, photographed in colour by Mr Pickering with great success. It seems churlish to say that the colours of Mr Beaufoy's photographs are not so good, when one considers the immense patience and skill he must have exercised to obtain these remarkable shots of living insects. The distribution of the plates in the volume is not good, necessitating continuous back and forward searches if the text references are to be followed up; and the numbering of the colour plates separately from those in black and white is little short of exasperating, particularly since in the fount used the arabic 1 is practically indistinguishable from its counterpart in roman type (cf. the references to the two Plates I on pp. 12 and 13 and the different type used for Plate 1 on p. 21). The editors would do well to change this system in the further volumes of this series and to secure that references to plates that are placed elsewhere in the text should be accompanied by page numbers.

There is no doubt that Dr Ford's book occupies a place of its own, not only in the literature on butterflies, but in the wider field of biology; and among its many good features is the lead he gives to naturalists to carry on with work to which he himself has already made such able and outstanding contributions. CYRIL DIVER

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W.1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November).

Selection and abstracting has been done voluntarily by H. F. Barnes, A. C. Evans, E. M. O. Laurie, E. Nelmes, W. S. Richards, H. N. Southern, H. V. Thompson and J. S. Watson; checking by B. M. Hobby.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

NIL

(*b*) Fresh water

Swaine, C. M. (1946). 'Records of Odonata from Flintshire (main part of county).' Ent. Mon. Mag. 82: 42.

Notes on localities and habitats.

Sims, R. B. (1945). *Sympetrum sanguineum* Müller (Odonata) in the Southern Fenland. J. Soc. Brit. Ent. 2: 249–50.

Very local form found dominant in area.

Lowndes, A. G. (1945). 'The swimming of *Euglena* and flagellar movement in general.' School Sci. Rev. 100: 319–32.

Evidence based largely on cinema photomicrographs of *Euglena viridis* and other monoflagellates in support of the view that during flagellar movement waves start from the base of the flagellum and travel towards the tip, increasing in both velocity and amplitude (thus indicating that at least some energy is generated in the flagellum itself) and accompanied by rotation. Since the flagellum is attached to the anterior end of the cell, the latter is caused to rotate and gyrate and so to move forward.

(c) Land

Lancum, F. Howard (1946). 'Wild animals and agriculture. 12. Some general observations.' J. Minist. Agric. 52: 563–6.

The final of this series of popular articles.

Lancum, F. Howard (1946). 'Wild birds and agriculture. 1. The crow family.' J. Minist. Agric. 53: 43–6.

The first of twelve monthly popular articles deals with the carrion crow (*Corvus corone*), magpie (*Pica pica*), jay (*Garrulus glandarius*), jackdaw (*Corvus monedula*) and raven (*Corvus corax*).

Lancum, F. Howard (1946). 'Wild birds and agriculture. 2. Hawks and falcons.' J. Minist. Agric. 53: 91–3.

Popular accounts of the buzzard (*Buteo buteo*), sparrow-hawk (*Accipiter nisus*), kestrel (*Falco tinnunculus*), merlin (*F. columbarius*), hobby (*F. subbuteo*) and peregrine falcon (*F. peregrinus*).

Harper, G. W. (1946). 'Lepidoptera of Sussex and West Hants, 1945.' Ent. Rec. 58: 1–5.

Records of occurrence, distribution and habitats.

Heath, J. (1946). 'The life-history of *Pachythelia villosella* Ochs. (=*nigricans* Curt.) (Lep., Psychidae).' Ent. Mon. Mag. 82: 59–63.

Heath-feeding moth restricted to the New Forest and south-east Dorset.

Fraser, F. C. (1945). 'Notes on *Trochilium crabroniforme* (Lew.) (Lepidoptera).' J. Soc. Brit. Ent. 2: 233–6.

This moth tends to form persistent colonies in old willows. Pupae crawl to edge of hole by cremasteric hooks and spines when ready for emergence. Details of pairing.

Jackson, R. A. (1945). '*Cucullia gnaphalii* in Hampshire.' Entomologist, 78: 14.

In certain Hampshire woods the cutting of timber gave great encouragement to the spread of golden-rod (*Solidago virgaurea*). In 1941 the moth *Cucullia asteris* was very common, and one larva of *C. gnaphalii* was also taken. By 1942 the golden-rod was mainly supplanted by St John's-wort (*Hypericum perforatum*), but a little golden-rod was left in the rides, on which a larva of *Cucullia gnaphalii* was found. Hampshire records for this species are very scarce.

Spooner, G. M. (1946). 'Hymenoptera aculeata from Charnwood Forest, Leicestershire.' Ent. Mon. Mag. 82: 25–9.

Notes on habitats and comparative distribution, on an area of Archaean rocks set in younger formations, east of the main Archaean massifs of Britain.

Benson, R. B. (1945). '*Emphytus basalis* (Klug) and some other interesting British sawflies (Hym., Symphyta).' Ent. Mon. Mag. 81: 101–3.

Distributional records, with some ecological data, of *Pamphilius histrio, P. latifrons, Calameuta filiformis, Arge rustica, Caliroa cinxia, Macrophya blanda, M. montana, Tenthredo dryas, Pristiphora albilabris, P. carinata, Emphytus basalis.* Gives key to British *Emphytus* species of the *cinctus* group.

Payne, R. W. (1946). 'Orthoptera in the Midlands.' Ent. Rec. 58: 9.

Distribution in Leicestershire, Rutland and Northamptonshire.

Callan, E. McC. (1945). 'Notes on some flea beetles from Slough, Bucks.' J. Soc. Brit. Ent. 2: 242–3.

Host plant records of 25 species of Halticinae.

Kaufmann, R. R. U. (1946). 'Preliminary notes on *Strangalia maculata* Poda (Col., Cerambycidae) and its aberrations in Great Britain.' Ent. Mon. Mag. 82: 115–17.

Distribution of this longicorn beetle is mainly England, rarer in north. Key to aberrations given.

Kaufmann, R. R. U. (1946). 'The distribution of *Phytoecia cylindrica* L. (Col., Lamiidae) in Great Britain.' Ent. Mon. Mag. 82: 17–18.

This longicorn beetle occurs south of the line River Severn to the Wash, but seems to be spreading northwards.

Grensted, L. W. (1946). 'Some Herefordshire Diptera.' Ent. Mon. Mag. 82: 15–16.

Nearly 100 species collected near Bromyard, with notes on ecology.

Grensted, L. W. (1946). 'An assemblage of Diptera on golden-rod.' Ent. Mon. Mag. 82: 35.

Eighty-five individuals collected; *Egle radicum* L. (Anthomyiid) was dominant (33), but Tachinids supplied 7 out of 27 species found on *Solidago virgaurea*.

Massee, A. M. (1945). 'Notes on some interesting insects observed in 1944.' Rep. E. Malling Res. Sta. 1944: 77–83.

Notes and observations on 21 species of insects and mites, including further notes on the distribution in England of the Tarsonemid mite of cereals (*Pediculopis graminum*) first recorded in Great Britain in 1944.

Ellenby, C. (1946). 'Ecology of the eelworm cyst.' Nature, Lond., 157: 451–2.

The number of larvae of *Heterodera rostochiensis* emerging from cysts stimulated with potato-root excretion was almost doubled when the latter were punctured, indicating that the protracted emergence is due to factors operating within the cyst and not to differences in the development of the eggs. It is suggested that the increased metabolism of the newly hatched larvae results in the accumulation of an inhibitor that prevents the development of the remaining eggs and appears to take effect through disturbances of the *p*H concentration, since no larvae emerged from cysts that were immersed, prior to stimulation, in acetate buffers of *p*H 3·4 or lower, and the numbers to emerge increased with increasing *p*H up to a concentration of 6·7 and then fell with a further increase in *p*H up to 8. Increased emergence also follows passage through the gut of earthworms, and this is shown to be due, at least in part, to the effect of digestive enzymes which may affect the cyst wall, egg-shell, larvae, or material between the eggs, causing changes in the rate of diffusion of the inhibitor.

Staniland, L. N. (1946). 'Potato root eelworm in the South-West.' J. Minist. Agric. 52: 538–41.

Distribution of *Heterodera rostochiensis* in Devon and Cornwall. Introduction is caused by soil and debris in seed potato bags, while spread is increased by the use of manure piles containing potato haulm and by the transplanting of broccoli.

(*d*) Small islands

Harrison, J. W. Heslop (1946). 'The geographical distribution of certain Hebridean insects and deductions to be made from it.' Ent. Rec. 58: 18–21.

Mainly a reply to a paper by Campbell, J. L., 1945, 'Distribution of *Zygaena filipendulae* and *Z. purpuralis* in the Hebrides', Entomologist, 78: 188.

Harrison, J. W. Heslop (1946). 'The Lepidoptera of the Hebridean Isles of Coll, Tiree and Gunna, with some remarks on the biogeography of the Islands.' Ent. Rec. 58: 57–61.

Believes Hebridean fauna contains both late glacial and early Boreal constituents in contradiction to Ford, E. B. 1946, 'Butterflies'. Appends a list of 110 species of Lepidoptera recorded from Coll, Tiree and Gunna.

Le Quesne, W. J. (1946). 'The butterflies of Jersey.' Ent. Mon. Mag. 82: 22–23.

Notes on occurrence and migration.

Le Quesne, W. J. (1946). 'The dragonflies of Jersey.' Ent. Mon. Mag. 82: 112–14.

No previous adequate list. The non-British species *Crocothemis erythraea, Lestes viridis, L. barbara* and *Sympycna fusca* were captured.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Amateur Entomological Society (1945). 'The amateur's library.' Amateur Ent. 8: 37–47.

Bibliography of entomological literature of interest to amateurs classified under General Entomology, Economic Entomology, Beekeeping, Microscopy, Botany and Orders of Insects.

Huxley, J. S. (1946). 'Species and evolution.' Endeavour, 5: 3–12.

A general discussion on the mechanisms of evolution.

Ford, L. T. (1945). 'Collecting Micros.' Amateur Ent. 8: 26–9.

Full details of collection and preservation of Microlepidoptera.

Charlson, S. (1945). 'Setting Micros.' Amateur Ent. 8: 29–31.

Methods for Microlepidoptera.

Jacobs, S. N. A. (1945). 'On the British species of the genus *Lithocolletis*, Hb.' Proc. S. Lond. Ent. Soc. 1944–5: 32–59. 1 pl.

Gives a description of each species of these micro-lepidoptera and a key for identification, also a table of food plants.

Cooper, B. A., Benson, R. B., Kerrich, G. J., O'Farrell, A. F. & Yarrow, I. H. H. (1945). 'Hymenopterist's handbook.' Amateur Ent. 7: 1–160.

A very full account of methods of collecting, rearing and preserving all major groups of British Hymenoptera, together with keys to the families.

Donisthorpe, H. (1946). 'British ants as at present known, with some remarks and a list of the same.' Ent. Rec. 58: 64–5.

Reviews Formicidae in Kloet & Hincks (1945), 'A check list of British Insects.'

Massee, A. M. (1946). 'The county distribution of the British Hemiptera-Heteroptera Supplement I.' Ent. Mon. Mag. 82: 94–5.

Additions and corrections to paper in (1945), Ent. Mon. Mag. 81: 253–73.

Duffy, E. A. (1946). 'Notes on the British species of *Pyrochroa* (Col., Pyrochroidae) with a key to their first-stage larvae.' Ent. Mon. Mag. 82: 92–3.

O'Farrell, A. F. (1945). 'Collecting dragonflies.' Amateur Ent. 8: 1–9.

Full details of collection, rearing and preservation of Odonata.

Classey, E. W. (1945). 'Collecting mosquitoes.' Amateur Ent. 8: 9–14.

Full details of collection, rearing and preservation of mosquitoes.

3. PARASITES

Spooner, G. M. (1946). '*Nomada errans* Lep., a bee new to Britain.' Ent. Mon. Mag. 82: 105–6.

A southern European species, inquiline of *Andrena nitidiuscula*, taken in Dorset at Durlston Head.

Fraser, F. C. (1946). '*Volucella* (Dipt., Syrphidae) larvae sp., breeding in a nest of *Vespula vulgaris* L. (Hym., Vespidae).' Ent. Mon. Mag. 82: 55–7.

See also O'Farrell, A. F., Woodcock, A. J. A. & Waller, G. (1946), Ent. Mon. Mag. 82: 57–8, for records of *Volucella zonaria* in Kent and Sussex.

Freeman, R. B. (1946). 'The pig as a host of *Pulex irritans* L. (Siphonaptera, Pulicidae).' Ent. Mon. Mag. 82: 19–21.

Several records of substantial human flea populations maintained on pigs.

Hill, M. A. & Gordon, R. M. (1945). 'An outbreak of dermatitis amongst troops in North Wales caused by rodent mites.' Ann. Trop. Med. Parasit. 39: 46–52.

Live *Haemogamasus oudemansi* and *Hypoaspis fenilis* were recovered from the bedding and straw-stuffed palliasses of the affected men, also dead unidentifiable mites. These and three other species of mites were found at the straw store, which was overrun with rats. The epidemic of dermatitis ceased immediately following steam disinfestation of the palliasses.

4. FOOD AND FOOD HABITS

Ellis, J. C. S. (1946). 'Notes on the food of the kestrel.' Brit. Birds, 39: 113–15.

A small collection of castings from one locality showed that the diet in a woodland-arable-grassland part of Yorkshire consisted through summer to early winter mainly of *Microtus*, but a spell of hard weather in February sent up the percentage of small birds.

Southern, H. N. (1945). 'The economic importance of the house sparrow, *Passer domesticus* L.: a review.' Ann. Appl. Biol. 32: 57–67.

The house sparrow has in the last hundred years more than doubled its range by introduction and spread chiefly into the grain-growing regions of the world. Recent data on diet exist for America and parts of Russia and Germany: grain may compose 75–80% of the food in arable areas, though much of this may be gleanings; in gardens and orchards the grain consumed is less, and garbage, weed-seeds and insects may take its place in varying proportions in different places. The diet of the nestlings is almost entirely insects at first. For Britain the data are either old or only doubtfully reliable.

Sims, R. B. (1945). 'Observation with a possible bearing on the prey of *Chrysopa phyllochroma* Wesm. (Neuropt.).' J. Soc. Brit. Ent. 2: 250–1.

This lacewing tends to feed on *Aphis fabae*, which may account for its distribution in more open country than other Chrysopidae.

Woolatt, L. H. (1946). 'Some biological notes on *Sciapteryx consobrina* Klug (Hym., Symphyta: Tenthredinidae).' Ent. Mon. Mag. 82: 18–19.

Apparently restricted to *Adoxa moschatellina*.

Shaw, H. K. Airy (1946). 'On some problems connected with *Hyalopterus dactylidis* Hayh. and *Hyalopteroïdes pallida* Theob. (Hem.-Hom. Aphididae).' Ent. Mon. Mag. 82: 30–5.

Both aphids live on cocksfoot grass (*Dactylis glomerata*) and may be conspecific. It is of interest to know whether the American species *Hyalopterus dactylis* originated in America or was introduced with the non-American cocksfoot grass, and whether either of these species will become a major cocksfoot pest in the country.

5. POPULATION STUDIES

Macintosh, N. A. (1946). 'The natural history of whalebone whales.' Biol. Rev. 21: 60–74.

A detailed account of the distribution, migrations, food and populations of twelve species of whales.

Chitty, D. & Shorten, M. (1946). 'Techniques for the study of the Norway rat (*Rattus norvegicus*).' J. Mammal. 27: 63–78.

Description of techniques for watching the feeding habits of rats, marking individuals, determining population size, and recording the rate of food consumption. Feeding was mostly nocturnal among well-fed rats, but among hungry animals could often be induced at any time of day. Changes in the objects or positions of objects present in the environment prevented feeding to an extent that varied with individuals and populations; but adjustment to artificial illumination was rapid. The number and duration of visits to the bait varied considerably among individuals. When hungry, the rats tended to begin feeding simultaneously and to eat faster and visit the bait more frequently than when full-fed. The average nightly consumption of wheat was estimated at 48 g. per rat, which is rather more than usual.

Lack, D. (1946). 'Clutch and brood size in the robin.' Brit. Birds, 39: 98–109, 130–5.

This detailed paper is based mainly on records sent in by correspondents and on other unpublished material. The peak of the breeding season occurs later in the more northern and eastern parts of Europe; the clutch size tends to rise to a peak in May and then fall again; the mean clutch size increases in a gradient from the Canary Islands (3·5) northwards to Scandinavia (6·3) and eastwards to Galicia (6·0); that even within Britain there are marked regional variations in hatching and fledging success. There is also some evidence, though not conclusive as yet, that clutches and broods vary from year to year. It is suggested that one of the main factors controlling the geographical clutch-size variation is the availability of food, either through its actual abundance or through the limits imposed on foraging time by latitude.

Lees, J. (1946). 'All the year breeding of the rock dove.' Brit. Birds, 39: 136–41.

Investigation of caves with breeding colonies of *Columba livia* in north Scotland showed that breeding occurs with a main peak in April and a period of quiescence in summer. Apart from this, breeding goes on most of the year, with subsidiary peaks in August, November and January.

Went, A. E. J. (1946). 'River Liffey survey VII. Salmon of the river Liffey.' Proc. R. Irish Acad. 51 B, no. 2: 9–26.

Discusses the proportion of the various age groups, the 'condition coefficient', sex ratio and correlation of length with river and sea life of salmon caught during the fishing season. The Liffey is essentially a spring fish river.

Greenslade, R. M. (1945). 'Observations on the life cycle of the apple blossom weevil (*Anthonomus pomorum* (L.) Curt.).' Rep. E. Malling Res. Sta. 1944: 83–92.

Details of the numbers of adults on the trees, buds with feeding punctures, buds with eggs, buds or blossoms with larvae, blossoms with pupae and of adults in capped blossom, together with the temperature hours above 50° F., in two-day periods during 1942.

Petherbridge, F. R., Stapley, J. H. & Wood, J. (1945). 'Wheat bulb fly field experiments.' J. Minist. Agric. 52: 351–4.

Includes figures of egg populations of *Leptohylemyia coarctata*.

Gross, F. & Smyth, J. C. (1946). 'The decline of oyster populations.' Nature, Lond., 157: 540–2.

It is suggested that the decline in populations of *Ostrea edulis* is due not to any one adverse environmental factor, but to their inability, following great reductions in numbers caused by overfishing and despite immense potential reproductive powers, to produce sufficient genetic variants to establish breeding stocks capable of adaptation to changing and adverse environmental conditions. This incapacity is attributed to the scattering of breeding individuals by overfishing as a result of which, owing to the immobility of the adults and the short duration of the pelagic larval stage, the chances of fertilization have become slight; where it does occur, it is likely to lead to the production of isolated highly inbred colonies. Active breeding ceases at temperatures below 15° C., but breeding stock and young oysters have been imported to British coasts from warmer waters; it is suggested that a more vigorous and adaptable stock should be built up by mass hybridization between a number of varieties from different geographical communities, especially from northern waters, followed by selection.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Benson, R. B. (1946). 'A mass-movement of the sawfly *Athalia cordata* Lep., in North Devonshire (Hym., Tenthredinidae).' Ent. Mon. Mag. 82: 87.

7. REPORTS OF ORGANIZATIONS

British Trust for Ornithology (1946). Twelfth Report. 15 pp.

Records of progress are given for various current field inquiries. Hatching and fledging data are now sufficient to allow preliminary analysis for some species: in the case of the blackbird (*Turdus merula*) about 50 young are fledged for every 100 eggs. Inquiries coming to an end are those on the wood-pigeon (*Columba palumbus*) and the rook (*Corvus frugilegus*); while information is still sought on nest sanitation and the spread of the fulmar (*Fulmarus glacialis*).

Gunton, H. C. (1945). 'Report on the phenological observations in the British Isles from December, 1943, to November, 1944.' Quart. J. R. Met. Soc. 71: PR1–PR31.

After a rather cold but not severe December, the year opened with a warm period lasting until mid-February. There followed, in southern districts, a cold and very dry period lasting until the beginning of April. In north-east and north-west districts the cold was much less pronounced. April was warm with considerably more than the average rainfall in the first three weeks; after this another period of deficient rainfall lasted until the end of June. In May there were marked fluctuations of temperature, and June was below the average. July was deficient in sunshine, day temperatures were mainly below, and night temperatures above the normal; rainfall for the month was above the average, but its incidence was mainly confined to the first half of the month. Early August was warm, dry and sunny, but a wet spell set in about the 19th and lasted till about 10 September with a decided drop in temperature at the end of this period. It was cool and dry for the remainder of September and beginning of October, but the rest of that month was wet and stormy and was followed by frost in early November. The principal differences in Scotland and Northern Ireland were snow at the end of February, March above average in temperature; May was wet particularly in the west. June was wetter while July and August were drier than in England. There was excessive rain in Scotland particularly in the south from September to November. Migrant birds arrived punctually in the spring. Native Lepidoptera were scarce after a mild winter when their natural enemies were active. Of the immigrant Lepidoptera, red admiral butterflies (*Vanessa atalanta*) were present inaverage numbers, painted lady butterflies (*V. cardui*) and silver Y moths (*Plusia gamma*) were scarce in the spring though the latter were seen in large numbers on the south coast in autumn.

Gunton, H. C. (1946). 'Report on the phenological observations in the British Isles from December, 1944 to October, 1945.' Quart. J. R. Met. Soc. 72: PR1–PR43.

A general description of the weather during this period is given. The cold spell in January retarded the appearance of early plants and insects, but the following sustained warm spell caused the appearance of some insects as much as three weeks before their usual date. Wasps were generally scarce, probably due to the cold spell at the end of April, since queens were numerous in the spring. Immigrant Lepidoptera were normal in abundance in early summer, but red admiral butterflies (*Vanessa atalanta*) and silver Y moths (*Plusia gamma*) were very plentiful in the autumn. Bath white butterflies (*Pontia daplidice*) were unusually numerous. With the exception of swallows and swifts which arrived late in the north, migrant birds generally appeared punctually.

Oundle School Natural History Society (1946). The Annual Report. 59 pp.

Includes phenological observations on insects, birds and frogs for 1945–6; brief reviews of work in 1945 in connexion with the British Trust for Ornithology's hatching and fletching inquiry, and a corn bunting survey; and of moths and butterflies observed during the year; general notes on birds, largely distributional; and a general list of freshwater invertebrates observed in local ponds and lakes during the past three years.